THE ESTIMATION OF BIOMASS IN A NATURAL STAND OF JACK PINE (*PINUS BANKSIANA* LAMB.)

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA

By

Thomas Ralph Crow

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DECEMBER 1970

TABLE OF CONTENTS

		PAGE
	LIST OF TABLES	iv
	LIST OF FIGURES	vii
I.	INTRODUCTION	
	A. Need for Biomass Estimates	1
	B. Objectives	2
	C. Essential Terms and Concepts	3
II.	SAMPLING CONSIDERATIONS	
	A. Biomass Distribution	
	1. Tree Size and Form	5
	2. Age	9
	3. Stand Density	10
	4. Site Quality	13
	B. Selection of Sample Individuals	16
	C. Sampling Individual Trees	22
III.	DESCRIPTION OF STUDY AREA	31
IV.	METHODS	
	A. Selection of Study Area	35
	B. Tree Measurements	35
	C. Understory Sample	36
	1. Establishment of Understory Plots	36
	2. Sampling Procedures for Understory Vegetation	37
	3. Soil Core Sample	38
	D. Litter Fall Sample	39
	E. Tree Harvest	40

TABLE OF CONTENTS, continued

PAGE

1. Selection 40
2. Root Excavation 41
3. Above-Ground Harvest 41
4. Laboratory Procedures 42

F. Units 43

V. RESULTS AND DISCUSSION

A. Mensurational Data for Study Plots 44

B. Preliminary Check of Individual Tree Sampling Techniques 44

1. Bole (wob) 44
2. Bole Bark 49
3. Canopy 49

C. Statistical Summary - Harvested Trees 54

D. Simple Allometric Functions 54

1. Needles 60
2. Live Branches 68
3. Cones and Dead Branches 73
4. Bole (wob) and Bole Bark 77
5. Roots 84
6. Total Tree 87

E. Multiple Regressions 90

F. Evaluation of Stand Estimate Techniques 93

G. Distribution of Organic Matter 105

1. Arboreal Layer 105

TABLE OF CONTENTS, continued

		PAGE
	2. Stand	107
	3. Litter Fall	112
	4. Macro-Litter	116
VI.	SUMMARY AND CONCLUSIONS	118
VII.	APPENDIX	121
VIII.	ACKNOWLEDGMENTS	128
IX.	LITERATURE CITED	129

LIST OF TABLES

TABLE PAGE

1. Relative distribution of biomass among components for three species of diverse form (Whittaker et al. 1963) .. 8
2. Relative distribution of biomass among components for Scots pine on different sites (Il'inskij 1968) 14
3. Deviation (%) of mean tree estimates from best estimate - balsam fir (Baskerville 1965b) 18
4. Deviation (%) of short-cut techniques from complete harvest - Japanese red pine (Satoo 1967b) 21
5. Deviation (%) from best estimate for "mean tree" estimates of canopy weight on three site classes - Eucalyptus (Attiwill 1966) 23
6. Climatic review for Itasca State Park 33
7. Mean stand and individual plot data (1967) 45
8. Mensurational data for trees selected for complete harvest 47
9. Comparison of actual to estimated bolewood biomass for each 5 ft sample section 48
10. Comparison of actual to estimated bole bark biomass for each 5 ft sample section 50
11. Vertical distribution of canopy weight 51
12. Statistical summary for harvested trees - canopy components 55
13. Statistical summary for harvested trees - bole components, roots, and complete tree 56

LIST OF TABLES, continued

TABLE PAGE

14. Coefficient correlations (r^2) for regression estimates of needle weight 61

15. Regression equations for estimation of oven-dry needle weight (g) 62

16. Comparison of regression equations for needle weight estimation - Kittredge and Crow 65

17. Coefficient correlations (r^2) for regression estimates of live branch weight 69

18. Regression equations for estimation of live branch weight (g) 70

19. Coefficient correlations (r^2) for regression estimates of dead branch weight 74

20. Coefficient correlations (r^2) for regression estimates of cone weight 75

21. Regression equations for estimation of dead branch and cone weight (g) 76

22. Coefficient correlations (r^2) for regression estimates of bole (wob) weight 78

23. Regression equations for estimation of bole (wob) weight (kg) 79

24. Coefficient correlations (r^2) for regression estimates of bole bark weight 82

25. Regression equations for estimation of bole bark weight (g) 83

LIST OF TABLES, continued

TABLE		PAGE
26.	Coefficient correlations (r^2) for regression estimates of root weight	85
27.	Regression equations for estimation of root weight (g)	86
28.	Coefficient correlations (r^2) for regression estimates of total tree weight	88
29.	Regression equations for estimation of total tree weight (kg)	89
30.	Simple linear correlation coefficients (r) between independent variables	92
31.	Comparison of "mean tree" estimates to every-tree summation	94
32.	Comparison of "mean tree" estimates to every-tree summation - above-ground components and total tree	95
33.	Comparison of dimensions for "mean trees" to mean stand DBH and tree height	97
34.	Exponential equations ($Y=AX^B$) for estimates of oven-dry weight	102
35.	Percentage of total weight by component and tree size	108
36.	Distribution of biomass among stand components - 1967	109
37.	Annual leaf litter production in coniferous stands	114
38.	Annual litter production in major climatic zones of the world (Bray and Gorham 1964)	115

LIST OF FIGURES

FIGURE PAGE

1. Curves for estimation of needle weight for jack pine in Minnesota - Kittredge and Crow 64

2. Distribution of total litter fall during sample period (July 7, 1968 to July 14, 1969). All sample weights prorated to a 30 day sampling period to provide a uniform time scale 117

I. INTRODUCTION

A. Need for Biomass Estimates

Formation of the International Biological Program (IBP) has promoted world-wide measurement and comparison of holistic properties for various terrestrial and aquatic communities with the hope of obtaining more complete knowledge of both internal and external controls that operate on all levels of organization within the ecosystem. Accurate biomass estimates are an important component in obtaining this knowledge. The forest ecosystem not only represents one of the most complex terrestrial systems but occupies a significant portion of the landscape, and thus can expect to receive major emphasis in the IBP.

Biomass estimates have both theoretical and practical utility. Rate of biomass accumulation in various ecosystems is of great interest to mankind since this fundamental energy-fixing process determines the ultimate quantity and quality of life supported within our biosphere. The first need when investigating the dynamics of water circulation, mineral cycling, and energy flow is an accurate estimate of the amount and distribution of organic matter, biomass, through which energy and matter are passed, converted, stored, and transferred to other organisms. Biomass accumulation is perhaps the best single indicator of the success of the biota within a particular environment.

Practical applications of biomass determination include estimates of fuel weight in forest-fire research. While moisture content, texture, compactness, and continuity of fuel, as well as prevailing weather conditions, also influence fire intensity, fuel weight is the most consistent factor and can be estimated readily (Brown 1963, 1965). With more intensive forest management, and increased utilization, along with more emphasis on production of woody material, biomass is considered a basic unit of measurement. Weight scaling of roundwood and chips has become well established in many sections of the country (Young and Chase 1965). Even the wise implementation of policy regarding forest resource utilization requires an understanding of forest ecosystem development and productivity; thus, accurate biomass determinations are important because of their link to understanding the dynamics of ecology.

Forest communities offer special problems in sampling biomass because of the size of individual trees and the complexity of stand structure. The intensity of sampling is necessarily very limited, and thus it is extremely critical that selected samples be truly representative of the forest population. In view of the number of studies that utilize biomass estimates, there is an obvious need to evaluate the adequacy of tree selection, sampling, and subsequent expansion to a stand estimate for a variety of species, community structures, and site conditions.

B. Objectives

The primary objective of this study was to evaluate the adequacy of various methods for the determination of plant biomass in a natural stand of jack pine (Pinus banksiana Lamb.). A secondary objective was to determine the distribution of plant biomass among the various components within the entire stand. Samples of woody, herbaceous, and moss components in the understory vegetation supplemented arboreal samples. Samples of litter drop and branch drop allowed an estimate of the magnitude of these components relative to the total standing crop.

C. Essential Terms and Concepts

Biomass is the total weight of living biological material per unit area at a given time. However, in forest communities, heartwood and bark may no longer be living material but are generally classified as biomass; dead roots and dead branches are excluded (Newbould 1967). The term standing crop is sometimes substituted for biomass when only a portion of the biological system, for example the above-ground portion, is considered (Westlake 1963). Phytomass refers specifically to the plant portion of the total biomass (Sukachev and Dylis 1964). Biomass is usually expressed in terms of dry weight, or ash-free (organic) weight. Although green weight is a convenient unit, its use should be avoided because moisture content varies greatly among species, among plant parts, and with weather conditions and time of sampling (Westlake 1963; Newbould 1967).

While major emphasis in this paper is on standing crop and biomass, reference will be made to production and productivity. Net primary production equals the increase of biomass per unit time minus any losses during this period. Major losses are from respiration, death of plants, consumption by insects and animals, and harvest by man. Gross primary production is then equivalent to the total assimilation of organic matter per unit time, including that used in respiration (Westlake 1963; Olson 1964; Newbould 1967). Production rate, the quantity divided by time (Q/T), is termed productivity. In comparison to net primary production recorded on a stand basis, the term apparent photosynthesis is used by Verduin et al. (1959) in reference to photosynthesis minus respiration in a particular organ or plant under observation. The CO_2 gas analysis of productivity is usually restricted to a single plant or organ and thus would determine apparent photosynthesis (Pearson 1965).

II. SAMPLING CONSIDERATIONS

A. Biomass Distribution

Realistically, the intensity of sampling for biomass has not been determined by desired statistical accuracy, but by the amount of time, money, and manpower available. Although these limitations can never be entirely eliminated, theoretically each component of biomass should be sampled relative to its importance to the ecosystem as a whole and its inherent variability. Less precision in sampling and measurement is necessary for minor components, but errors must be minimized in sampling major components.

Relative distribution of biomass among tree components has been reported to change with tree size and form, age, stand density, site conditions, species, past silvicultural treatment, climate, and season. These variables are obviously not independent, as for example, size and form vary with stand density, age, and species; thus, division of these factors for discussion must be somewhat arbitrary and according to their discussion in the literature.

1. Tree Size and Form

Although dry matter naturally increases with increasing tree size, the relative distribution of biomass among components is not constant.

In a 35 year-old Scots pine (Pinus sylvestris L.) plantation, Ovington and Madgwick (1959a) found the percentage of bole weight decreased with increasing tree size (DBH range--6.5 to 21.5 inches) with a corresponding increase in percentage of crown and root weight.

Baskerville (1965b) recorded similar trends for a 42 year-old natural stand of balsam fir (Abies balsamea (L.) Mill.). Bolewood accounted for 63.9% of the total dry weight in a one inch balsam fir, but decreased to 39.9% of a 10-inch tree. Within the same DBH range, the proportion of foliage dry weight increased from 3.3% to 16.3%, and branch weight (wood and bark) increased from 2.8% to 15.3%. Proportions of stem bark and roots did not change significantly. Stem bark represented about 7% of the total dry weight with only a slight decrease in larger trees. Roots gradually declined from 23.3% to 21.3% of total dry weight over the range of diameters.

Baskerville's results are surprising only in that percentage bark did not change significantly with changes in tree size. Decreasing proportions of bark with increasing stem size are well documented. In contrast to the 7% of total dry weight represented by bole bark with balsam fir, bark of speckled alder (Alnus rugosa (DuRoi) Spreng.), beaked willow (Salix bebbiana Sarg.), and high bush blueberry (Vaccinium corymbosum L.) represented 30 to 38% of total dry weight (Dyer, Chase, and Young 1968). Volume tables for unpeeled, second-growth jack pine prepared by Brown and Gevorkiantz (1934) indicate a linear decrease from 24% of total weight represented by bark for a one-inch (DBH) tree to 11% for a 12 inch tree.

Koršun (1940) also indicated a marked reduction in bark percentage with increasing tree size. Among 200 Norway spruce (Picea abies (L.) Karst.) ranging from 10.6 to 55.6 cm in diameter, percentage bark decreased from 14.7% of total weight to 4.5%, an average of two percent for each 10 cm increase in DBH. Again, percentage of branch weight increased with increasing tree size (from 3.2 to 35.9%); branch percent increased an average of 2% for each 0.1 increase in the DBH/height ratio. Burger (1940) noted the amount of branchwood increased more rapidly than foliage with increasing bole diameter in an 80 year-old European beech (Fagus sylvatica L.) stand. Kuroiwa (1960a) reported still another foliage/total weight increase with increasing tree size in a 20 year-old fir (Abies mariesii Mast.) stand (percentage of total dry weight for suppressed: intermediate: codominant: dominant = 18.5 : 20.8 : 21.8 : 27.2%).

Obvious variations exist in branching forms and crown structures among species. Ovington (1956) found conifers, especially spruce, had up to five times more branches per unit length of bole than hardwoods of comparable height. Despite greater average branch weights for hardwoods, conifers usually have greater weight in branches due to their greater frequency of branching. For red pine, needle weight averaged 43% of total live crown weight, compared to only 21% for jack pine on the same site--a marked difference between the species (Brown 1965). Whittaker, Cohen, and Olson (1963) provide an excellent comparison of the relative distribution of biomass among components for three species of diverse form, yellow-poplar (Liriodendron tulipifera L.), white oak (Quercus alba L.), shortleaf pine (Pinus echinata Mill.) (Table 1). Yellow-poplar, a tall, clear-stemmed tree with a conical crown and small branches, is intermediate in almost all respects between white oak with its rounded crown and heavy branches, and shortleaf pine with its long, clear bole, and narrow, pyramidal crown.

Table 1. Relative distribution of biomass among components for three species of diverse form (Whittaker et al. 1963).

Biomass Distribution (%)	*Liriodendron tulipifera*	*Quercus alba*	*Pinus echinata*
Stem wood	76.4	58.5	80.1
Stem bark	9.2	12.5	8.9
Branchwood and bark	12.2	26.9	7.5
Current twigs and leaves	1.9	2.1	1.5
Second-year leaves	--	--	1.8
Third-year leaves	--	--	0.2
Fruit	0.3	0.02	0.01

The effects of form and structure on productivity are more subtle. According to Ovington and Pearsall (1956), evergreen species in three plantations in Great Britain had a significantly greater annual yield than deciduous species, with the deciduous larch intermediate. This difference was accounted for by longer periods of photosynthesis made possible by a persistent canopy and by the conical canopy, which allowed greater exposure of existing assimilating surfaces. In deriving an equation relating absorbed radiant energy and geometric crown form, Jahnke and Lawrence (1965) considered the effective crown surface area as a cone under changing angles of incidence.

Extending the comparison of biomass distribution as a function of form, Whittaker et al. (1963) analyzed 10 dominant and codominant deciduous trees in the manner applied to shrubs by Whittaker (1961, 1962). Along a size gradient from small shrubs to medium-sized trees, Whittaker et al. reported (1) increasing proportions of biomass in woody structures with a corresponding decrease in foliage and fruit fractions, and (2) decreasing proportions of biomass in roots with wide species variation.

2. Age

Ovington (1956) and Satoo (1967b) cite changes in relative biomass distribution as a function of age, and apparently independent of other factors. According to Satoo, leaf and branch percentage decreases with age. Satoo was rather contradictory when he stated within the same paragraph that (1) percentage of underground biomass was stable for the age span (13 to 46 years) studied in the development of Japanese red pine (<u>Pinus densiflora</u> Sieb. and Zucc.) plantations and (2) root percentage increases with age. Ovington stated that the ratio of bole to canopy increases with tree age. Since both leaf area index (Möller 1945) and root weight per unit volume of soil (Kittredge 1948) quickly reach full site occupancy and remain relatively constant through stand maturity, one would expect both leaf and root biomass percentages to decline relative to total stand biomass with age.

In terms of total dry matter productivity in forest stands, Ovington (1956) associated maximum productivity with development of the pole stage when maximum horizontal and vertical crown development results in full occupancy of the site, and thus better site utilization. Within the forest community, arboreal dominance is greatest during the pole stage and the development of the understory is at a minimum. The understory makes its greatest contribution during juvenile and mature stages of the forest (Smith 1962).

3. Stand Density

Relative proportions of most tree components vary with changes in stand density.

In a study of natural stands of balsam fir, Baskerville (1965a) found the following trends in percent of total standing crop per acre from lowest density (700 stems per acre) to highest density (5000 stems per acre):

a. foliage decreased from 16.4 to 12.8 percent;

b. branches decreased from 17.4 to 10.1 percent;

c. bolewood increased from 57.1 to 67.1 percent. No trends were found for cone and stem bark weight. In a 26 year-old red pine (Pinus resinosa Ait.) plantation, Heiberg, Leyton, and Loewenstein (1959) reported 62 percent of the standing crop in bolewood at 8 ft spacing compared to 70 percent at spacings of 3 ft, 4 ft, and 6 feet. Decreases in percent foliage and increases in percent bolewood with increasing stand density were recorded for plantations of Japanese red pine (Senda et al. 1952; Satoo, Nakamura, and Senda 1955) and plantations of eastern white pine (Pinus strobus L.) (Senda and Satoo 1956). With increasing density in red pine plantations, Hutnik (1964) also found proportionately more biomass in bolewood and less in leaves and branches.

Sampling a 10 year-old jack pine plantation, Adams (1928) found that dry weight of needles for an average tree at 8 ft spacing was almost 11 times that for the average tree at 2 ft spacing; branch dry weight at 8 ft spacing exceeded that at 2 ft spacing by nearly 18 times. The average pine in the 8 ft spacing contained the most dry matter, but heavy branches reduced the relative amount of bole biomass compared to trees grown in closer spacings. Close spacing also altered the natural lateral development of roots into a more penetrating type of root system. At 2 ft spacing, dry weight of lateral roots exceeded that for tap roots by only 1.5 times, compared to 2 times in 4 ft spacing, and 13 times in 6 ft spacing.

From studying the effect of density on agricultural crop yield, Iwaki (1958) indicated the ratio for non-photosynthetic systems (stems, roots, and reproductive organs) to photosynthetic systems (leaves) increased with greater density in earlier stages of growth, but found no apparent correlation between this ratio and density in later stages.

While there is agreement concerning a decrease in foliage relative to total biomass with increasing tree density, there is some disagreement concerning absolute weight of foliage per unit area as a function of density. Senda et al. (1952) and Senda and Satoo (1956) found fresh weight of foliage per unit area in pine stands to remain relatively constant for all densities, thus agreeing with Möller's (1947) assertion that the total amount of foliage in a closed stand is relatively constant regardless of density. In contrast, Baskerville (1965a) did find a weak but significant trend towards increasing amounts of foliage with increasing density with the tolerant balsam fir.

Two theories concerning the effect of stand density on productivity are generally recognized. Based on analyses of yield tables and European thinning experiments, Assmann (1961) hypothesized that current annual growth per unit area increased with increasing stocking until optimum production is reached at a definite density. According to Assmann, optimum production occurred within a narrow range of densities, and only on the best sites would this range become broad. Möller (1945,1947,1954) and Möller, Müller, and Nielsen (1954a,1954b) hypothesized that production increases with increased stocking up to full occupancy of the site. But within wide limits beyond full occupancy, increased density did not significantly affect annual growth, only its distribution among components within the stand. Only at extremely high densities would crowding become limiting. Derivation of this hypothesis is from theoretical considerations of the relationship between photosynthesis and respiration in forest stands. This hypothesis was also tested by Möller and others in Europe with thinning studies in stands of Norway spruce and birch (Betula verrucosa).

4. Site Quality

Site quality incorporates the multitude of interdependent soil-climatic-biological factors that affect the productive capacity of vegetation. Accumulation of biomass per unit area is probably the best indicator of plant success as a function of site quality. In forestry, indexes based on height-age relationships are commonly used despite widely recognized deficiencies. In terms of total dry matter production, height growth does not seem to be much of a site indicator (Adams 1928; Baskerville 1965a). Baskerville questioned the validity of site indexes based on height-age relationships for tolerant species after he found total stand production to vary inversely with the average height of dominants (age constant) in balsam fir stands. Burger (1940) stressed the need to consider total standing crop and total annual production per unit area to gain a more complete comparison of yield capacity of different sites.

Il'inskij (1968) studied absolute and relative distribution of biomass among tree components for Scots pine on four different sites (Table 2). The trends in percentage of total tree biomass from best to poorest site were: stem - decreasing; bark - no trend; branches - no trend; needles - slight increase; cones - no trend; dead branches - increasing; above-ground tree biomass - decreasing; roots over 30 mm -

Table 2. Relative distribution of biomass among components for Scots pine on different sites (Il'inskij 1968).

Components	Site Classes[a] I	II	III	IV
	Percent - Dry Weight			
Stem	68.13	64.15	63.16	58.42
Bark	6.74	7.52	6.45	6.08
Branches	5.42	6.09	6.47	4.58
Needles	1.20	1.55	1.58	1.95
Cones	0.12	0.12	0.05	0.20
Dead branches	0.54	1.02	1.49	1.75
Total Above-Ground	82.15	80.45	79.20	72.98
Roots less than 30 mm	6.82	4.43	3.30	2.05
Roots greater than 30 mm	5.22	7.49	7.33	8.87
Root stock	5.81	7.63	10.17	16.10
Total Below-Ground	17.85	19.55	20.80	27.02
Grand Total	100	100	100	100

[a]Site I - best site.

increasing; roots under 30 mm - decreasing; root stock - increasing; total below-ground biomass - increasing.

Satoo (1967a) found quantity of leaves in closed stands of Japanese cedar (Cryptomeria japonica D. Don) increased linearly with increased site quality. Kittredge (1944) also stated that quantity of leaves is larger on better sites. Crowns of jack pine and red pine on good sites held more foliage per unit weight of branchwood than those from poor sites (Brown 1965). In contrast, however, quantity of leaves did not vary systematically with site quality in natural stands of European beech and Norway spruce (Möller 1945), or in plantations of Norway spruce in Japan (Satoo 1967a).

Total accumulation of biomass within the phytocoenose and to some extent its distribution among components is indicative of various climatic regions. In a spruce-birch tundra forest with 137 metric tons/ha of total biomass, perennial above-ground organs (mainly bole) represent 72% of the total biomass, green portions 7%, and roots 21% (Rodin and Bazilevich 1967). From studies of coniferous and mixed forests reviewed by Rodin and Bazilevich, the maximum accumulation of biomass is 358 metric tons/hectare. In mature coniferous and mixed forests, assimilating organs of trees, shrubs, grasses, and mosses account for 3 to 9% of the total biomass; slightly greater percentages are cited for young communities, hydric forest communities, and open forest communities with well developed ground flora. Perennial above-ground components account for 70-80% (60% in young communities), and roots average 22% of total biomass. Biomass accumulation up to 500 metric tons/ha is reported by Rodin and Bazilevich for mature stands of deciduous forests. Percentage of green assimilating organs for the deciduous forest stands ranged between 1.5 and 3% (5% in young communities), approximately half that for coniferous forest communities. Above-ground perennial components again ranged between 70 and 80% and roots account for 15-25%. The maximum accumulation of biomass cited by Rodin and Bazilevich, 1724 metric tons/ha, is for a mountain evergreen tropical forest in Brazil. An average figure cited for tropical rain forests, 517 metric tons/ha, is greater than the maximum figure cited for deciduous forests. Comparison of average figures for a tropical rain forest to other major formations indicates a greater percentage of total biomass in green assimilating organs (9%), similar proportions in perennial above-ground components (72%), and lower percentages in roots (19%).

B. Selection of Sample Individuals

Forest biomass sampling schemes involve two critical steps: (1) selection and (2) sampling of individual trees. The accuracy of extrapolating from the individual(s) to a stand estimate, is entirely dependent (1) on selection of individuals, or possibly an individual, which accurately represents the entire population and (2) on accurate sub-sampling of the individual tree or trees.

Selection of trees for destructive sampling ranges from a single "average" tree to large numbers selected on the basis of a stand table. Ovington (1956) selected a single tree with average dimensions. Wilde (1967) analyzed several trees of average height and diameter. Ovington and Madgwick (1959b) divided the sample population into five diameter classes and selected four trees close to the midpoint from each of the classes. Weetman and Harland (1964) selected six suppressed, eight intermediate, and six dominant trees for analysis. Golley, Odum, and Wilson (1962) based regression curves on 10 trees representing the most abundant diameter classes. The biomass for the midpoint of each DBH class was calculated and multiplied by the number of trees in the class. Heiberg, Leyton, and Loewenstein (1959) harvested 60 trees to derive regression curves for red pine. Six trees close to the mean diameter of the stand were cut from 10 different plots. Baskerville (1965b) felled more than 100 trees to regress biomass and DBH and derive a stand table for biomass using integral DBH classes. Rennie (1966) favors selection of sample trees of mean basal area, with consideration of the number of samples necessary to give stand estimates within predetermined confidence limits.

In comparing various "short-cut" methods to an every tree summation in a 42 year-old balsam fir stand, Baskerville (1965b) clearly demonstrated potential errors when using average tree techniques. Using regression equations for each component (foliage, branches, cones, stem wood, stem bark, roots), Baskerville determined the biomass for all 188 trees in a 0.2 acre plot and converted the total to a per acre basis. In comparison to this figure, estimates of biomass per acre based on a single tree of mean height, mean diameter, mean basal area, mean volume, or the average codominant tree, varied as much as ± 50% (Table 3). Use of the tree of average volume did result in only a 0.1% overestimate of total tree biomass per acre, but errors in estimates of individual components per acre were as great as 12.8%.

Table 3. Deviation (%) of mean tree estimates from best estimate - balsam fir (Baskerville 1965b).

Base of Estimation	Foliage	Branches	Cones	Stem Wood	Stem Bark	Total Above-Ground	Roots	Total Tree
Tree of mean height	-63.5	-64.3	-59.0	-45.2	-47.5	-51.2	-47.5	-50.2
Tree of mean diameter	-43.6	-44.6	-36.7	-24.5	-27.3	-30.8	-26.8	-29.8
Tree of mean basal area	-24.1	-26.4	-16.0	-7.1	-9.7	-12.9	-9.8	-12.2
Stand table	-1.6	-2.0	-2.6	-2.5	-0.6	-2.1	+2.9	-1.0
Tree of mean volume	-12.7	-12.8	-2.6	+4.3	+1.9	-1.1	+4.1	+0.1
Average codominant tree	+42.4	+49.4	+58.5	+48.5	+48.0	+47.7	+48.7	+47.8

The stand table estimate, based on a regression estimate for each integral DBH class and multiplied by the frequency within the class, resulted in only a 1.0% underestimate for total biomass and a maximum error of +2.9% for roots.

Ovington and Madgwick (1959b) reached similar conclusions based on a comparison of three methods of stand biomass determination in a 37 year-old Scots pine plantation. Stand estimates were based on (1) a single tree of average DBH, (2) the average tree from each of five diameter groups, (3) an every-tree summation based on regression analysis. In comparison to method (3), (1) and (2) underestimated stand biomass. Method (2), similar to a stand table approach, gave a close estimate.

In an 8 year-old Monterey pine (Pinus radiata D. Don) plantation, Ovington, Forrest, and Armstrong (1967) compared a complete sample to estimates based on various unit area samples, average tree samples, and regression estimates. Because of the great structural diversity within a stand, the probability of obtaining a representative unit area is small and thus Ovington et al. concluded this method to be inaccurate and ineffective. For example, estimates of bole biomass, the most important stand component, using unit area samples were less accurate than crown estimates simply because canopies covered 90% of the entire surface area and boles only 0.3%. The "effective canopy" technique (Bray 1960) utilized by Bray and Dudkiewicz (1963) is a good example of unit area sampling. The canopy area of each tree is staked-out and mapped on graph paper. Tree biomass per unit area is then equal to the weight of the tree divided by its effective canopy area.

Estimates based on average trees were most effective when trees were selected from the entire size range and a marked improvement was noted when estimates were weighted according to frequency within a class. Ovington et al. (1967) stress that even regressions of high significance can be derived by chance for a particular set of samples. A regression analysis based on a stratified random sample according to the frequency within a class reduces this potential error.

Satoo (1967b) measured the total biomass in a 4 by 5 m plot in a 15 year-old natural stand of Japanese red pine, and compared this estimate to estimates based on: (1) the regression of dry weight to DBH for all trees; (2) the tree of mean cross-sectional area; (3) the ratio of the sum of cross-sectional areas of selected trees to the stand cross-sectional area; (4) the regression of dry weight to DBH for selected trees (Table 4). Errors from use of the tree of mean basal area were much less than those cited by Baskerville (1965b) for the all-aged stand of balsam fir. It is evident that "average tree" techniques may be valid for certain community structures and study requirements. Further evaluation of the use of mean trees such as presented by Attiwill (1966) will help make this decision.

Kuroiwa (1959), Ovington and Madgwick (1959b), Baskerville (1965b), and Attiwill (1966) all noted that the variable B in the general relationship

$$\log_{10}\text{Dry Wt.} = \log\ A + B\ \log_{10}\text{DBH}$$

will vary with the component, and thus selection of the mean tree will depend on the component to be studied. Using the expression

Table 4. Deviation (%) of short-cut techniques from complete harvest - Japanese red pine (Satoo 1967b).

Base of Estimation	Foliage	Branches	Stem Wood	Above-Ground	Total Tree
Allometric relation for all trees	+8.7	+10.5	+3.5	+4.8	+3.3
Tree of mean cross-sectional area	-3.5	-6.9	+3.8	+5.6	-0.7
Ratio of cross-sectional area	+9.5	+13.8	+1.2	+3.5	+3.5
Allometric relation for selected sample trees	+5.1	+13.3	+2.9	+4.3	+5.1

$$\left(\frac{\sum_{i=1}^{i=n'} DBH^{B}}{n'} \right)^{1/B}$$

n' = number of trees/unit area, B = the variable B in the allometric relationship

which is the DBH of the tree of mean dry weight, Attiwill (1966) has demonstrated the following inequalities: DBH of the tree of mean branchwood weight > DBH of the tree of mean leaf weight > DBH of the tree of mean basal area which, in turn, is greater than the mean stand diameter. Thus selection of the mean diameter for the sampling unit will result in a significant underestimate of canopy weight. The tree of mean basal area, a more logical sampling unit, may still result in serious error, depending upon basal area distribution and stem form. Attiwill further demonstrated that total canopy weight for Eucalyptus (Eucalyptus obliqua L'Herit.) increased according to the cross-sectional area of the bole at the canopy base (or the cube of DBH) rather than basal area, a factor of DBH^2. A comparison of these three series of estimates (Table 5) to the best estimate, a summation of predicted crown weights of n' trees per ha, supports the above contentions.

C. Sampling Individual Trees

Once sample trees have been selected, criteria must be established for fractionation of components and subsequent sampling.

Rennie (1966) listed three factors to be considered when dividing components. (1) Non-commercial and commercial components should be separated so that information can be provided on various logging

Table 5. Deviation (%) from best estimate for "mean tree" estimates of canopy weight on three site classes - Eucalyptus (Attiwill 1966).

Base of Estimation	Site Index 84	Site Index 102	Site Index 107
Tree of mean DBH	-33.4	-31.1	-41.3
Tree of mean basal area	-16.9	-18.1	-22.8
Tree of mean cross-sectional area at the crown base	-4.3	-3.0	-3.7

methods. Data could still be grouped for more theoretical considerations. (2) Fractions should be of reasonable anatomical and physiological homogeneity. (3) Fractionation should be practical. Extensive subdivision of needles and branches by age groups is extremely time consuming and difficult, thus the potential error through respiration losses should be considered. Rennie also questioned the practicality and utility of root extraction. In most cases extraction is so difficult, according to Rennie, that results are suspect and of little value. At the minimum four main components (leaves, branches, trunk, roots) should be recognized and separated (Newbould 1967).

Before felling a sample tree, crown spread should be measured. Following felling, Newbould (1967) recommends measurement of total height, crown height, DBH, and bole diameter below the lowest living branch. Bole diameter at tree base, diameter at the bole midpoint, and diameter at the base of the contiguous crown are also useful measurements.

Subsampling of the bole generally consists of disks or pie-shaped wedges removed from the center or end of each section. In sampling balsam fir, Baskerville (1965a) removed a disk from each of the upper 11 internodes, one disk from 1.5 ft below the 11th internode, and then a disk every 3 ft to the base. This was found to be more than adequate with specific gravity determinations reduced to every third section, except for the two bottom sections. In contrast, Young and Chase (1965) removed only four disks in determining the bole biomass of seven tree species ranging from 5.6 to 15.8 inches in diameter.

A 1 to 2 inch disk was removed 6 inches above the tree base, the middle of the merchantable bole, 6 inches below the top of the merchantable bole, and a 2 to 4 inch disk was removed at the midpoint of the total bole height. Cole, Gessel, and Dice (1967) sectioned the trunk into 3 m lengths and removed a 5 cm disk from each section. Stem bark is often separated from the sample disks and considered independently from the bole. Tree age and annual increment can be determined from the base disk.

Canopy sampling schemes generally regard the crown as a homogeneous solid with little consideration of variation in structure, morphology, or changes with age (Stiell 1962). Hall (1965) and Madgwick (1967) could conclude only that foliage distribution within red pine canopies was extremely erratic and varied greatly among trees. Again with red pine, Stiell (1962) and Stephens (1969) were more specific. In a vertical gradient from top to canopy base, Stiell found foliage weight to increase until mid-crown, remain constant for four or five whorls in most trees, then decrease toward the canopy base. The four or five whorls of constant needle weight in mid-crown generally contained half to three-quarters of the total foliage weight. In a study of 10 plantations, Stephens noted similar vertical foliage distribution (by weight) despite great differences in site, stand density, DBH, height, and crown length. Foliage distribution was generally symmetrical and normal with its mean near the crown midpoint and standard deviation equal to 1/5 of crown length. Pearson (1966) suggested that with fewer leaves in the lower canopy, total leaf weight varies in proportion to the square root of canopy height. In selecting samples to estimate branch and needle weight for jack pine, Brown (1965) separated branches from the upper 2/3 of the canopy from those of the lower 1/3; the latter had a lower proportion of needle to branchwood weight.

In canopy sampling, leaves, live branches, and dead branches are usually separated. To overcome obvious difficulties in separating and measuring leaf and branch weight, several techniques have been developed to correlate a destructive subsample to the entire sample population. For example, Rennie (1966) developed a relationship between green weight of large branches and oven-dry weight for a subsample of convenient size. Baskerville (1965a) found a linear relationship between oven-dry weight and air-dry weight for foliage and twigs of balsam fir, white spruce (Picea glauca (Moench) Voss), and paper birch (Betula papyrifera Marsh.). To facilitate estimating the weight of branches and foliage (foliage = small twigs and leaves), Ando et al. (1959) grouped branches according to their horizontal stratification within the crown. Within each group a primary subsample was selected and weighed; the fraction of branches was then separated and weighed. From the primary sample, a secondary subsample of leaves and small twigs was separated and the weight of each determined. The total weight of branches equalled:

$$\text{(total strata wt.)} \times \frac{\text{(branch wt. - primary sample)}}{\text{(total wt. - primary sample)}}$$

Total leaf weight equalled: (total strata wt.) X

$$\frac{\text{(foliage wt. - primary sample)} \times \dfrac{\text{(leaf wt. - secondary sample)}}{\text{(foliage wt. - secondary sample)}}}{\text{(total wt. - primary sample)}}$$

Twig weight was also estimated using a similar formula.

There are no short-cut methods for root sampling. Support roots can be dug, winched, or washed out. Rootlets have been sampled by taking soil cores (Bray, Lawrence, and Pearson 1959), but estimates must be considered as stand biomass. Ashing root samples to determine organic weight can eliminate problems in separating inorganic particles adhering to the roots. Once sufficient samples have been removed to relate root weight and root diameter, the relationship can be applied to the ends of broken roots and thus speed sampling (Whittaker 1962).

Numerous regressions relating weight of various components to a parameter such as DBH or branch diameter have been developed. Often cited is the curvilinear relationship developed by Kittredge (1944) between foliage weight and DBH for ponderosa pine (*Pinus ponderosa* Laws.) in California:

$$\log_{10}W = 1.67 \log_{10}D - 0.73$$

W = dry weight of foliage (kg)

D = diameter (inches).

A similar formula was developed by Cable (1958) for ponderosa pine in central Arizona:

$$\log_{10}W = 1.8811 \log_{10}D - 0.8882$$

where all units are the same as in Kittredge's formula. Based on data presented by Hansen (1937) for jack pine in Minnesota, Kittredge (1948) cited:

$$\log_{10}W = 2.87 \log_{10}D - 1.58.$$

Kittredge (1944) studied 10 species in 28 different stands on a variety of sites and concluded the relationship between leaf weight and diameter to be valid for trees of different sizes, densities, crown classes, and ages until at least culmination of growth and beyond this point for tolerant species of all-aged stands.

Numerous studies have further documented Kittredge's conclusion. For example, both leaf weight and branch weight were found to be logarithmic functions of DBH in a 25-40 year-old aspen (Populus davidiana) stand (Satoo, Kunugi, and Kumekawa 1956) and a 28 year-old Japanese cedar plantation (Satoo and Senda 1958). Green needle weight, oven-dry needle weight, and needle surface area were all logarithmic functions of DBH in plantations of Zelkova (Zelkova serrata Mak.) (Satoo, Negisi, and Senda 1959). In eastern Tennessee, logarithmic relationships were established between leaf weight and diameter for trees in a mixed oak forest (Rothacker, Blow, and Potts 1954), short-leaf pine (Olson 1959), and several hardwoods, spruces, and fir (Shanks and Clebsch 1962).

D^2H (Ogawa, Yoda, and Kira 1961; Ogawa et al. 1965a; Ogawa et al. 1965b) or D^2+H+D^2H (Newbould 1967) as independent variables may yield better correlations than DBH. Other independent variables include volume (V) of crown when considered as a paraboloid

$$W = 10.62\ V + 1403.5 \quad (W = \text{dry wt. foliage (g)};\ r = 0.970)$$

and the product of the crown length and width expressed in square feet (A)

$$W = 54.0\ A - 836.4 \quad (W = \text{dry wt. foliage (g)};\ r = 0.970)$$

where both are based on data from red pine (Stiell 1962). Kittredge (1948) found air-dry weight (kg) of needles (W) for jack pine in Minnesota to be a linear function of five year periodic growth (G):

$$W = 23.1\ G - 0.1.$$

Leaf weight per branch and branch weight of Eucalyptus were related to branch diameter (Attiwill 1962):

$$\log_{10}LW = 1.6607(\log_{10} X) + 1.8167$$

LW = leaf dry weight (g)

X = branch diameter (inches)

$$\log_{10}Y = 2.3790(\log_{10}X) + 1.4668$$

Y = total dry weight of branchwood (g)

X = branch diameter (inches).

Among numerous independent variables considered (DBH, tree height, crown height, bole length, DBH X crown length, DBH X tree height, DBH X bole length), DBH and crown length X DBH resulted in the most precise relationship with crown weight per tree for jack pine and red pine (Brown 1965).

Regressions of bole and root weight to a measurable parameter have also proven successful. The relation between dry weight of roots and D^2H for elm (Ulmus parvifolia) saplings was:

$$\log R = 0.913 \log D^2H + 0.6915$$

where R equals dry weight of roots in g, D equals diameter at stem base in cm, H equals tree height in cm (Tadaki and Shidei 1960).

Among commonly recognized fractions, the regression correlations for cones and dead branches are the poorest. These components, however, are minor in weight and resulting errors are small relative to total biomass.

While significant correlations are apparent for a wide variety of circumstances, application of a common regression equation beyond a single species and study site is limited. Because of the effects of spacing on relative proportions of biomass, Stiell (1962) questions the use of a single correlation relating crown weight to DBH for more than one density or spacing. Regression coefficients not only vary among species but may vary between stands of the same species where age or density of stems is variable (Satoo et al. 1958, 1959; Satoo 1962). Regression coefficients also vary with season. For example, the correlation between green leaf weight (kg) and DBH (cm) for Japanese red pine (Maruyama and Satoo 1953) based on fall samples

$$\log W = 1.30 \log D - 0.59$$

differs from the correlation based on spring samples

$$\log W = 1.82 \log D - 1.07.$$

Madgwick (1968) also found regression coefficients to vary with sampling date in a 17 year-old Virginia pine (*Pinus virginiana* Mill.) stand. Despite the many variables that affect correlations, Ogawa et al. (1965b) did find it valid to apply a common regression for 50 species of similar life form in a tropical rain forest.

III. DESCRIPTION OF STUDY AREA

Three study plots were located on land owned by Northwest Paper Company in SW/SE and SE/SW of Section 4, Township 143 North, Range 34 West (Lat 47 deg, 15 min N; Long 95 deg, 05 min W) in northwestern Hubbard County, 2 1/2 miles north of Lake George in north-central Minnesota.

Characteristics of the jack pine study area include: (1) the single-layered structure of almost pure jack pine, (2) very few shrubs, but a high frequency of small, evergreen, prostrate or "half-shrubs" such as bearberry (Arctostaphylos uva-ursi (L.) Spreng.) and wintergreen (Gaultheria procumbens L.), (3) a high frequency of relatively few species. These characteristics are common to the more xeric jack pine sites in the Lake States. In addition, many species of high frequency - bearberry, wintergreen, haircap moss (Polytrichum juniperinum Hedw.), reindeer lichen (Cladonia sp.), wild oats grass (Danthonia spicata Lam.), bedstraw (Galium boreale L.), aster (Aster laevis L.) - are closely associated with poor-site jack pine in the Lake States (Hansen 1946). A complete floral list is presented in Appendix Table 1. Regional classification of the vegetation type includes Central Pine Unit recognized by the Northcentral Forest Research Station (Chase 1964), and Great Lakes Pine Forest (Küchler 1964). The study area can also be classified as a jack pine cover type which is defined by the Society of American Foresters (1954) as a northern forest type in which 50% or more of the dominant or codominant trees are jack pine. In accordance with the classification of upland forest communities in

Itasca State Park (Kurmis and Hansen 1969a,1969b), the vegetation on the study site was the jack pine - bearberry type.

The climate of the study region is distinctly continental, with warm, humid summers and cold, dry winters. Based on records at Itasca State Park (7 miles west of Lake George), the mean annual precipitation is 24.66 inches and the mean annual temperature is 38.7 F (Baker and Strub 1965; Baker, Haines, and Strub 1967). A complete climatic description is presented in Table 6.

The topography of the study area is level to slightly rolling. Soils are deep, uniform, noncalcareous, fine to medium glacial outwash sands of the Menahga loamy sand series (Arneman 1963). Typically, these soils have a shallow dark layer of incorporated organic matter, concentration of plant roots in the upper 2 inches, loose single grain structure in all horizons, indistinct horizon boundaries, and tend to be xeric.

Analyses of soil samples taken from the study plots are presented in Appendix Table 2.

Table 6. Climatic review for Itasca State Park.[a]

Climatic Factor		Source
Annual precipitation (1912-1965)		(Baker et al. 1967)
Mean	24.66 inches	
Median	23.80 inches	
Mode	21.55 inches	
Range	13.93 inches (1929)	
	35.51 inches (1949)	
Mean monthly precipitation (1931-1960)		(Baker et al. 1967)
January	0.75 inches	
February	0.62 "	
March	1.23 "	
April	2.31 "	
May	3.36 "	
June	4.18 "	
July	3.58 "	
August	3.50 "	
September	2.08 "	
October	1.51 "	
November	1.30 "	
December	0.83 "	
Percent precipitation during summer (June, July, August) - 45%		
Mean annual snowfall - 50 inches		(Baker et al. 1967)
Number of days/year with snow cover greater than one inch (1949-1965)		120-130 days
Mean annual temperature	38.7 F	(Baker and Strub 1965)
Mean daily maximum	50.7 F	(Baker and Strub 1965)
Mean daily minimum	27.8 F	(Baker and Strub 1965)
Absolute maximum	105.0 F	(Baker and Strub 1965)
Absolute minimum	-51.0 F	(Baker and Strub 1965)
Mean daily maximum of hottest month (July)	80.8 F	(Baker and Strub 1965)

Table 6, continued

Mean daily minimum of coldest month (January)	-5.4 F	(Baker and Strub 1965)
Mean monthly temperature (1931-1960)		
January	6.6 F	
February	10.4 F	
March	22.1 F	
April	39.1 F	
May	52.2 F	
June	61.6 F	
July	67.6 F	
August	65.1 F	
September	55.5 F	
October	44.7 F	
November	26.5 F	
December	12.9 F	
Mean number of frost free days	- 96	(Baker and Strub 1963)

[a] Elevation 1500 ft.

IV. METHODS

A. Selection of Study Area

The single-stratum, monospecific forest of even-aged jack pine selected for this study is a community of relatively simple structure, and potential problems in the sampling and estimation of biomass are thereby greatly reduced. A poor site was selected so that the size of individual trees would be small enough to make harvesting feasible for a single worker. Additional criteria for selection of a site include lack of disturbance by grazing and thinning, and uniformity of soil characteristics, topography, and microclimate. The selection of the Lake George site from 31 jack pine stands checked during the summer of 1967 was also based on the accessibility of the area and proximity to laboratory facilities at the University of Minnesota Forestry and Biological Station at Itasca State Park.

Based on site index and average stand age for the delineated area, normal stocking in stems per acre for a fully stocked jack pine stand was determined from Wackerman, Zon, and Wilson (1929). Three 0.1 acre plots were then established as close to full stocking, 60 trees per 0.1 acre, as possible.

B. Tree Measurements

All trees within the three 0.1 acre plots were numbered and tagged, and the following parameters recorded:

(1) crown position (suppressed, intermediate, codominant, dominant),

(2) DBH to nearest 0.1 inch with vernier diameter tape,

(3) total height and crown height to nearest ft using a Haga altimeter,

(4) average crown spread to nearest 0.1 ft,

(5) age of tree as determined from a core taken one ft above ground level.

Crown spread was measured with a leveled periscope with the top mirror removed; measurements were taken along the cardinal directions and averaged. True age of the jack pine was taken as the age at one ft plus 4 years (Hansen 1946). Measurements of crown height included both distance from crown tip to lowest green branch and from crown tip to base of contiguous crown. The latter distance was subtracted from total height to obtain bole height.

C. Understory Sample

1. Establishment of Understory Plots

Within each 0.1 acre arboreal plot, rectangular plots were located for sampling biomass of understory vegetation. Selection of the rectangular plots as opposed to the traditional quadrats was based on work by Christidis (1931), Clapham (1932), and Pearsall and Gorham (1956). Each found ractangular strips to be more effective than quadrats for sampling homogeneous vegetation. In sampling standing crop in fen and reedswamp vegetation, Pearsall and Gorham (1956) used a transect plot of contiguous quadrats in order to transect the floristic pattern and to reduce the "edge" effect. After sampling the frequency of certain species within a defined area utilizing both square and elongated plot shapes, Clapham (1932) recommended a rectangular strip 4 m by 0.25 m as the more effective shape. According to Christidis (1931), the rectangular shape insures minimum variation among plots and maximum variation within plots.

Use of transects with randomly located starting points as opposed to a larger number of randomly scattered quadrats also reduces the potential of trampling damage to plots yet to be sampled. Since work other than understory sampling was to be undertaken simultaneous within the same 0.1 acre plots, this was an important consideration.

Understory plots consisted of six 0.5 ft by 2 ft contiguous subplots, resulting in a transect 12 ft long and 0.5 ft wide. To account for any biomass change during the growing season, two sets of samples were taken. The first three subplots were harvested beginning June 24, 1968, the second three beginning August 16. Sampling was completed on September 5 and before any killing frost.

2. Sampling Procedure for Understory Vegetation

Within each subplot all live shrubs, herbaceous plants, mosses, and lichens were removed. Following rain or heavy dew, vegetation was allowed to dry before sampling. Vegetative materials were clipped at ground level and sealed in polyethylene bags to reduce transpiration losses. In the laboratory, materials were sorted into woody, herbaceous, and moss-lichen components; green weights were taken and materials were oven-killed.

Enormous amounts of dead litter incorporated within the harvested mosses and lichens made it necessary to separate these materials by hand; thus, rapid weighing and killing was not always possible.

Following killing, harvested materials were resealed in polyethylene and stored. Constant oven-dry weights (at 105 C) were obtained later that fall when a large, very efficient forced-air oven was available for use.

3. Soil Core Sample

After removal of vegetation within each subplot, a soil core 10 cm in depth was extracted from two diagonally opposite corners of the rectangular subplot. These cores were intended to sample the massive concentration of herb and shrub roots, tree rootlets, and rhizomes observed within the rather thin rhizosphere and thus supplement estimates based on excavation of tree roots. Before core extraction, all remaining organic materials were removed, exposing mineral soil at the sample point. Two samples per subplot resulted in a 203 cc sample.

Advantages in using a soil core sampler were:

(1) the consistency of soil volume sampled,

(2) the rapidity of the sampling technique,

(3) the ease of handling and transporting the volume of soil sampled,

(4) the minimal amount of equipment required for sampling.

The core method must, however, be used in conjunction with other root sampling techniques because of its inadequacy in sampling the large, concentrated root systems of trees.

Again, extracted samples were sealed in polyethylene bags for transportation to the laboratory. Adequate separation of mineral and organic materials was obtained by the following procedures. (1) The bulk of mineral soil was removed by washing samples through a 1.5 mm mesh screen. Kneading the polyethylene bags before removal of soil facilitated breakdown of soil aggregates. (2) After washing, residual materials were brushed off the screen onto newspaper and oven-dried. The resulting mixture, however, still included a substantial amount of mineral particles which had adhered to root hairs or were too large to pass through the screen. (3) Further separation involved flotation in which samples were rewetted and thoroughly blended using a Hamilton Beach malt mixer. After allowing time for mineral particles to settle, floating organic material was removed, material still in suspension was filtered out, and settled particles discarded. Samples were oven-dried to a constant weight at 105 C.

D. Litter Fall Sample

On each 0.1 acre arboreal plot, eight litter traps were established in June 1968 in a random position. Traps were constructed from 24 inch wide, 4 mil polyethylene sheets, and heat sealed to form a cylinder 3.75 ft in circumference. Bags were made rigid by no. 9 wire strung through a heat sealed fold at one end of the cylinder. The other end was gathered and tied with string. Heat sealing was accomplished with a hot iron, with kraft paper used to insulate the plastic from direct heat. Traps were secured to three lath stakes by one inch bolts placed through the polyethylene sheeting just under the wire frame and secured on the inside of the bag by a 2 inch piece of lath tightened against the wire frame by a washer and nut. The resulting traps, 21 inches in depth and 36 inches from mouth of trap to ground level, proved to be both exceptionally sturdy and high enough to remain above the snow level. Each trap was emptied monthly throughout the year. Needles, small twigs, and strobili were separated and both air-dry and oven-dry (105 C) weights determined.

Larger litter such as branches, less frequent in time and space, were collected within a 0.05 acre plot established in the center of each 0.1 acre arboreal plot. These areas were cleared of fallen material and stakes were located along the perimeter of the plots.

E. Tree Harvest

1. Selection

To insure a representative sample selection, 40 trees for harvest were randomly selected from the four crown classes in proportion to the number of individuals within each class. Combination of the three 0.1 acre plots resulted in a crown class distribution of 17 suppressed, 58 intermediate, 72 codominant, and 33 dominant trees. The ideal sample distribution--4 suppressed, 13 intermediate, 16 codominant, 7 dominant--was followed as closely as possible.

While destructive sampling continued throughout the field season, the harvest was designed to allow full shoot elongation before canopy sampling. The sampling schedule was:

(1) June - July, 20 trees - root excavation,

(2) late July - August, 20 trees - complete harvest,

(3) August - September, 20 trees - above-ground harvest.

Thus, among the 60 trees felled, 40 root systems were excavated, 40 above-ground systems were harvested, with 20 complete trees removed.

Among the 20 complete trees harvested, the sampling distribution was 3 suppressed, 6 intermediate, 7 codominant, and 4 dominant.

2. Root Excavation

Excavation of roots was relatively easy in the loose, sandy subsoil; smaller trees could be manipulated to provide leverage, pulling support roots and many rootlets intact from the loose subsoil. All cut or broken root ends were then excavated; surface laterals smaller than 0.5 inches in diameter were ignored as these were harvested with the root core sample.

3. Above-Ground Harvest

Trees selected for bole and canopy harvest were dropped onto a cloth tarpaulin. Partial excavation of the root system allowed a controlled drop and thus minimized loss of material during felling. The size of the trees allowed a complete canopy harvest. Branches were removed, and dead branches were separated from branches with live needles. For ease of handling, branches were cut into small segments and sealed in polyethylene bags. The bole was sectioned into 5 ft lengths and a terminal section of variable length. From the base of each 5 ft section, a 3 inch disk was cut for specific gravity and bark weight determinations.

As with other samples, materials were oven-killed as soon after harvest as possible, restored in polyethylene bags, and stored for future oven-drying to a constant weight. To handle the daily bulk of arboreal samples to be oven-killed, a plywood box (50 X 30 X 30 inches), insulated with an asbestos-silica fire-resistant material

(Marinite - John-Manville Co.) and heated to 70-80 C with a two burner hot-plate, was constructed.

4. Laboratory Procedures

For oven-drying, materials were placed in unbleached muslin bags. Dislodgement of needles from twigs and separation of the two components required (1) vigorous shaking of the muslin bags following oven-drying and (2) brushing these now independent components through a coarse 6 mm screen. The brittle oven-dried needles were easily broken and passed through the screen, the twig and branch fragments remained. Cones were also separated and weighed independently.

The oven-dry weight of each 5 ft bole section was based on the 3 inch disk subsample. Following oven-drying of the disk, the laboratory procedure consisted of: (1) weighing total disk, (2) removing bark and reweighing disk to determine bark weight and bole weight without bark (wob), (3) determining diameter of each disk, (4) measuring width of the disk and calculating bark weight/unit surface area for disk, (5) determining volume of disk by water immersion technique, (6) calculating specific gravity of disk.

Estimated oven-dry weight of the bole (wob) for each 5 ft section equalled:

(volume of the frustum of a cone)(mean specific gravity)

$$\text{volume} = \pi h/3(r_1^2 + r_1 r_2 + r_2^2)$$

Estimated oven-dry weight of bark for each 5 ft section equalled:

(curved surface area of the frustum of a cone)(mean bark weight/area)

$$\text{surface area} = \pi\,(r_1 + r_2)\sqrt{h^2 + (r_1 - r_2)^2}$$

For the formulas, specific gravity and bark weight/unit surface area for each section was an average of the base disk and the succeeding disk. The oven-dry weight of the variable length terminal segment was added to the calculated bole weight (wob) for total bole weight (wob).

F. Units

Estimates of biomass/area are expressed in metric units, generally kg/hectare. Conversion to lb/acre is facilitated by multiplying kg/ha by 0.892 (1 kg = 2.205 lb; 1 ha = 2.471 acres). Biomass is expressed in terms of oven-dry weight (105 C); estimates should be increased by 1% to obtain weights at 85 C (Andersson 1970) and 2% to obtain weights at 70 C (Forrest 1968).

Statistical tests of significance are expressed at the 0.05 (*) or 0.01 (**) probability level; mean values ($\bar{X}$) are given with a plus or minus one standard error of the mean ($\pm$ SE).

Throughout the paper, the symbol DBH^2 refers to the square of the bole diameter at breast height (4.5 ft); D^2H refers to the DBH^2 multiplied by total tree height. As previously defined, the term bole (wob) refers specifically to bolewood without the bark.

V. RESULTS AND DISCUSSION

A. Mensurational Data for Study Plots

Complete stand and individual plot data based on 1967 measurements are in Table 7. The three 0.1 acre plots, all within a contiguous area, differ slightly in mean tree dimensions with plot C > plot B > plot A. Mean and standard error of mean for the stand, a combination of the three 0.1 acre plots, reflect the relatively small individual tree size and even-aged character of the stand: mean DBH = 4.77 ± 0.083 inches; mean total height = 38.11 ± 0.423 ft; mean age = 51.32 ± 0.363 years; N = 180. The stand had a basal area of 78.49 ft^2/acre and a site index of 40.57 feet at 50 years.

Because trees were harvested from the entire size range of the population and in proportion to the distribution within each crown class, mean parameters for the harvested trees compare favorably to stand means: mean DBH = 4.68 ± 0.174 inches; mean total height = 37.55 ± 0.849 ft; mean age = 49.85 ± 0.808 years; N = 40.

B. Preliminary Check of Individual Tree Sampling Techniques

1. Bole (wob)

Planned destructive sampling of individual trees involved complete root and canopy harvesting, but subsampling of the bole. To evaluate the adequacy of an estimate based on a single 2-3 inch disk from each 5 ft bole section, above-ground portions of a codominant tree, C21, and an intermediate tree, C40, were completely harvested.

Table 7. Mean stand and individual plot data (1967).

Parameter	Mean ± Standard Error of Mean			
	Plot A	Plot B	Plot C	Total Plot
Number of live trees /0.1 A	59	60	61	180
DBH (inches)	4.45 ± 1.14	4.79 ± 1.08	5.06 ± 1.07	4.77 ± 0.08
Total height (ft)	35.93 ± 5.83	38.20 ± 5.64	40.11 ± 4.83	38.11 ± 0.42
Crown height - contiguous crown	17.16 ± 4.41	16.75 ± 5.12	18.17 ± 4.63	17.36 ± 0.35
Crown height - bottom live branch	20.98 ± 5.36	20.62 ± 6.75	19.93 ± 5.16	20.51 ± 0.43
Average crown spread (ft)	6.15 ± 1.87	6.68 ± 2.10	7.21 ± 2.11	6.71 ± 0.18
Age	49.10 ± 4.89	51.45 ± 4.65	53.34 ± 4.15	51.32 ± 0.36

Mensurational data for the two trees is in Table 8.

Usual subsampling techniques were followed; however, the entire section along with its subsample were oven-dried (105 C) to a constant weight. To expedite oven-drying of this massive sample, each 5 ft section was further subdivided, with all sawdust and bark chips included in the drying bag.

A comparison of estimated biomass to actual biomass (Table 9) indicates the subsample procedure as outlined in the Methods section to be adequate. Total oven-dry bole weight (wob) was overestimated by only 2.88% for C40 and 1.30% for C21. Among those geometric solids which potentially represent the physical form of a bole section—cylinder, paraboloid, cone, and neiloid--the frustum of a cone (a truncated cone) was selected. Selection was based on the validity of the model and the convenience of volume calculation using the form. Errors for individual bole sections reflect differences between the model used for volume determination and the actual physical form. Basal sections with flaring butts represent a truncated neiloid and thus biomass estimates based on the frustum of a cone are significantly larger than actual biomass for both trees. Middle sections of the bole are best represented by a truncated paraboloid (Chapman and Meyer 1949) which will have a slightly larger volume than a truncated cone. A comparison of estimated values to actual weights does not reflect a consistent underestimate; however, a general compensation of the overestimate for the basal section does occur. Small top logs supposedly resemble a truncated cone (Chapman and Meyer 1949), although the weight of the upper section was overestimated based on a

Table 8. Mensurational data for trees selected for complete harvest.

Parameter	Tree Number C21	Tree Number C40
Crown class	codominant	intermediate
Age (1969)	55	55
Total height (ft)	41.5	34.0
Crown height (ft) - contiguous	23.4	21.3
Crown height (ft) - lowest green branch	23.4	14.0
DBH (inches)	5.1	4.2
Diameter (inches) - tree base	7.3	5.6
Diameter (inches) - base of contiguous crown	3.5	2.8

Table 9. Comparison of actual to estimated bolewood biomass for each 5 ft sample section.

Tree and Section Number	Bole (wob) Oven-Dry Weight (G)		
	Actual	Estimated	Percent Deviation
C21 (1)	7096.0	8315.64	+17.18%
(2)	6408.6	5727.12	-10.63%
(3)	5103.2	4791.99	-6.09%
(4)	4081.3	4253.67	+4.22%
(5)	3265.8	3258.42	-0.04%
(6)	2053.8	1913.59	-6.82%
(7)	949.8	1078.66	+13.56%
(8)[a]	353.7	353.7	--
Total	29312.2	29692.79	+1.30%
C40 (1)	5001.1	5518.92	+10.35%
(2)	4002.7	3912.29	-2.25%
(3)	3369.7	3341.51	-0.83%
(4)	2630.9	2634.72	+0.14%
(5)	1653.2	1754.21	+6.10%
(6)[a]	818.8	818.8	--
Total	17476.4	17980.45	+2.88%

[a]Variable length terminal section - actual oven-dry weight added to estimates for 5 ft sections.

truncated cone for both C21 and C40.

Accurate bolewood estimates are of prime importance since this component commonly represents 50% or more of the total tree biomass.

2. Bole Bark

Based on previously described techniques, estimates of oven-dry weight of bole bark exceeded the actual oven-dry weight by 6.3% for C40 and 5.8% for C21 (Table 10). Again the pattern was a large overestimate of bark biomass for the basal section with underestimates for succeeding sections. Although bole bark estimates were not as satisfactory as bolewood estimates, the 6% error was considered acceptable relative to the total importance of the biomass component.

3. Canopy

Although a complete canopy harvest was anticipated, separation of the canopy into one ft divisions based on the origin of branches along the bole allowed a cursory evaluation of potential canopy subsampling techniques.

Vertical distribution of canopy weight proved to be very erratic for both C40 and C21 (Table 11), making the formation of adequate subsampling techniques difficult.

Considering the one ft divisions within the contiguous canopy, divisions (2) through (15) for tree C21 and (2) through (9) for tree C40, an estimate based on a sample of even-ft divisions, a 50% sample, resulted in a +4.03% divergence from actual total canopy (needles and branches) oven-dry weight for C21, and a +3.95% divergence for C40. Selection of odd-ft divisions would result in an underestimate of the

Table 10. Comparison of actual to estimated bole bark biomass for each 5 ft sample section.

Tree and Section Number	Bark Oven-Dry Weight (G)		
	Actual	Estimated	Percent Deviation
C21 (1)	1762.5	2536.39	+43.90%
(2)	998.6	1044.57	+4.60%
(3)	935.9	844.66	-9.74%
(4)	784.9	636.43	-18.91%
(5)	614.2	471.14	-23.29%
(6)	388.7	292.54	-24.73%
(7)	186.2	173.40	-6.87%
(8)[a]	---	---	---
Total	5671.0	5999.13	+5.8%
C40 (1)	1047.1	1392.9	+33.02%
(2)	623.2	558.90	-10.31%
(3)	467.0	410.48	-12.10%
(4)	351.8	322.68	-8.27%
(5)	265.9	244.49	-8.05%
(6)[a]	---	---	---
Total	2755.0	2929.46	+6.3%

[a]Variable length terminal section - bark not separated.

Table 11. Vertical distribution of canopy weight.

Vertical Section (Ft)		Oven-Dry Weight (G)			
Number	Feet	Total	Needles	Branches	N/B
Tree Number - C21					
(1)	0-24[a]	0	0	0	--
(2)	24-25	400.6	71.1	327.5	0.217
(3)	25-26	670.0	117.8	547.3	0.215
(4)	26-27	470.0	85.3	365.9	0.253
(5)	27-28	207.1	67.5	136.9	0.493
(6)	28-29	809.9	262.8	535.0	0.491
(7)	29-30	908.0	197.8	709.1	0.279
(8)	30-31	215.9	77.8	133.0	0.585
(9)	31-32	391.7	140.8	239.0	0.589
(10)	32-33	560.8	137.4	195.9	0.701
(11)	33-34	420.5	163.8	216.6	0.756
(12)	34-35	210.3	92.8	109.3	0.849
(13)	35-36	374.3	163.8	184.1	0.890
(14)	36-37	545.0	242.0	227.0	1.066
(15)	37-38	294.2	149.5	111.8	1.337
(16)	38-tip[b]	542.0	316.6	189.0	1.675
Tree Number - C40					
(1)	0-21[a]	544.6	283.3	253.1	1.119
(2)	21-22	470.0	85.3	365.9	0.233
(3)	22-23	661.5	159.0	461.5	0.344

Table 11, continued

Vertical Section (Ft)		Oven-Dry Weight (G)			
Number	Feet	Total	Needles	Branches	N/B
(4)	23-24	410.9	165.6	210.4	0.787
(5)	24-25	245.8	58.7	155.1	0.378
(6)	25-26	510.1	155.3	285.9	0.543
(7)	26-27	856.0	288.1	397.1	0.725
(8)	27-28	722.0	340.1	257.0	1.323
(9)	28-29	189.0	88.7	66.8	1.328
(10)	29-tip[b]	640.2	368.1	228.1	1.614

[a]Base of tree to base of contiguous crown.

[b]Variable length.

same magnitude. On the assumption that middle canopy whorls represent a median sample, selection of two sections near the middle of the canopy resulted in the following divergence from actual oven-dry weight of total canopy:

a. tree - C40

sections sampled - (4) and (6)

expansion factor - 4

divergence = -9.37%

b. tree - C40

sections sampled - (5) and (7)

expansion factor - 4

divergence = +8.41%

c. tree - C21

sections sampled - (6) and (8)

expansion factor - 7

divergence = +14.37%

d. tree - C21

sections sampled - (7) and (9)

expansion factor - 7

divergence = +44.92%

Based on the selection technique utilized, the acceptability of the ± 10% error produced from a 25% sample (a and b) would depend on the requirements for each individual study. The potential for error using a 14% sample (c and d) is, however, unacceptable.

The steady increase in the ratio of needle weight to branch weight, N/B in Table 11, indicates the necessity of subsampling all vertical sections of the canopy. Morphological as well as structural characteristics of the canopy must be considered in devising accurate subsampling techniques.

C. Statistical Summary - Harvested Trees

The statistical summary for each tree component (Tables 12 and 13) allows an initial comparison of relative importance and variation for each tree component.

Mean oven-dry weight for the complete tree was 44.22 ± 5.52 kg, of which 25.52 ± 2.17 kg was bole (wob) biomass. The order of importance following bole (wob) in terms of mean oven-dry weight is tree roots, bole bark, live branches, needles, dead branches, and cones.

The largest relative variation as measured by the coefficient of variation was for cones, 86.4%, followed by live branches, 73.8%; dead branches, 68.7%; needles, 62.3%; roots, 56.2%; complete tree, 55.8%; bole (wob), 53.8%; bole bark, 45.5%.

For all components, the median was smaller than the mean, indicating a slight positive skewness in sample weight distribution.

D. Simple Allometric Functions

To investigate the allometric relationships between biomass for jack pine components and a number of independent variables, six curve forms were fitted and correlation coefficients calculated using the GE-235 time-sharing computer program CURFT$. The forms of the fitted curves are:

linear, $Y = A + BX$ (1)

Table 12. Statistical summary for harvested trees - canopy components.[a]

Parameter	Cones (G)	Dead Branches (G)	Live Branches (G)	Needles (G)
Mean	383.75	1290.28	4221.03	3097.48
Standard deviation	331.70	886.39	3116.87	1929.54
Standard error of mean	52.44	140.14	492.78	305.06
Coefficient of variation (pct)	86.44	68.70	73.84	62.29
Smallest variate	0.0	366.8	445.5	197.6
Largest variate	1191.0	4397.8	13678.8	9016.1
Median	280.5	1026.9	3196.4	2759.3
Total range	1191.0	4030.7	13233.3	8818.5

[a]N = 40.

Table 13. Statistical summary for harvested trees - bole components, roots, and complete tree.[a]

Parameter	Bole (wob) (Kg)	Bole Bark (G)	Roots (G)	Complete Tree (Kg)
Mean	25.522	4447.83	7164.95	44.217
Standard deviation	13.721	2022.99	4024.71	24.690
Standard error of mean	2.169	335.64	636.31	5.520
Coefficient of variation (pct)	53.76	45.48	56.17	55.84
Smallest variate	4.264	910.9	1864.4	15.180
Largest variate	67.762	10428.8	19240.9	111.482
Median	23.922	4219.16	6603.9	38.688
Total range	63.498	9517.93	17376.5	96.302

[a]N = 40 - bole and roots; N = 20 - complete tree.

exponential, $Y = Ae^{BX}$ (2)

$Y = AX^{B}$ (3)

hyperbolic, $Y = A + B/X$ (4)

$Y = 1/(A + BX)$ (5)

$Y = X/(A + BX)$ (6)

For the least squares regression fit, non-linear equations were transformed into linear forms:

$\ln Y = \ln(A) + BX$ (2)

$\ln Y = \ln(A) + B \ln(X)$ (3)

$Y = A + B(1/X)$ (4)

$1/Y = A + BX$ (5)

$1/Y = B + A(1/X)$ (6)

Upon completion of the analysis, an inverse transformation is performed to obtain required quantities in the proper form. For example, the coefficient A in the linear form of equation (3) is

$A' = \ln(A)$.

Following inverse transformation, A is

$A = e^{A'}$.

Note that there is no need in this case to transform B since $B = B'$.

The relative closeness of the relationship between two variables is usually measured by the coefficient of determination (r^2) for linear relationships or by the index of determination (i^2) for curvilinear relationships (Ezekiel and Fox 1959). These indices indicate the proportion of variance in the dependent variable associated with differences in the independent variable. Several qualifications must be recognized, however, to make valid comparisons and interpretations of curves based on i^2 and r^2 values. (1) The coefficient and index of determination are defined for the special situation in which Y and X each follow a normal distribution and the universe of all possible paired values of Y and X form a bivariate normal distribution. If a completely random sample were drawn from such a universe, the coefficient or index calculated for that sample could be regarded as an estimate of true correlation existing in the universe. When original or transformed values of X and Y are not distributed in a "normal" fashion, r^2 or i^2 may still be a rough estimate of correlation in the universe, but no longer is it certain that formulas appropriate to the normal distribution still apply. Logarithms and reciprocals of X and Y do form a bivariate normal distribution (Ezekiel and Fox 1959). (2) Selection of values for the independent variable, especially non-random selection, can strongly influence the coefficient or index value. A high value will result if only extremely large and extremely small values of X are chosen, and a low value is obtained if the chosen values of X are concentrated within a narrow range (Ezekiel and Fox 1959). (3) The usual coefficient or index of fit can be used to compare equations with the same form of the dependent variable, but are not suitable when the form of dependent variables differ. It is not entirely valid to compare the r^2 value of a linear equation

$$Y = A + BX$$

to the i^2 value of a logarithmic equation

$$\log Y = \log A + B \log X$$

even though the same dependent and independent values are used to fit the equations (Furnival 1961). Thus, r^2 and i^2 values were used in this study only as a general indicator of the relationship between variables. For selected relationships, standard error of estimate ($S_{y/x}$), confidence limits, and deviation of estimated values from measured values were calculated to supplement the evaluation of relationships. In addition, a comparable index (R^2) based on a common scale, calculated values of Y instead of transformed values of Y, was also utilized:

$$R^2 = \frac{\sum(y'-\bar{y})^2 - \sum(y'-Y)^2}{\sum(y'-\bar{y})^2}$$

Y is the estimated value of the dependent variable; y' is the actual value of the dependent variable; $\bar{y}$ is the mean of the actual (y') values.

For convenience, the differentiation between the coefficient of determination (r^2) and index of determination (i^2) will not be made in the text. All coefficients, regardless of curve form will be referred to as coefficients of determination (r^2).

Several characteristics of regression curves also need recognition. (1) A fitted regression merely describes the trend between two variables within the sample range. An obvious linear trend within these limits may not be linear beyond the sample data; thus, potential errors are great when extrapolating beyond observed values of the independent variable (Freese 1964). (2) Because the fitted regression is a sample-based estimate and subject to sampling variation, confidence limits should be computed for any predictions made from the regression (Freese 1964).

All regressions discussed in the text are highly significant ($P < .01$) unless otherwise stated.

1. Needles

The strongest correlation or closest relationship in terms of r^2 was obtained using DBH^2 X total tree height (D^2H) as the independent variable in the linear regression (Tables 14 and 15). Evaluation based on the standard error of estimate and R^2, however, indicates the curvilinear function

$$Y = AX^B \qquad (3)$$

using the same independent variable to be slightly superior in fit:

$Y = AX^B$ $\qquad X = D^2H$

$S_{y/x} = 560.953$ g (18.11% of mean Y)

$R^2 = .9195$

$Y = A + BX$ $\qquad X = D^2H$

$S_{y/x} = 571.798$ g (18.46% of mean Y)

$R^2 = .9166$

The curvature is so slight, however, that the straight line function is a practical approximate of the relationship over the relatively small size range represented in the even-aged stand. The obvious exponential trend between the independent variable D^2H and oven-dry weight of needles as shown by Baskerville (1965a) for balsam fir is certainly not evident for the Lake George jack pine stand.

The linear transformation of

$$Y = AX^B, \qquad (3)$$

$$\log Y = \text{Log } A + B \log X \quad \text{or} \quad \log Y = a + B \log X, \qquad (3)$$

where X equals the DBH is perhaps the most commonly cited regression form for estimating dry weight of foliage. In comparing slope and Y-intercept constants for equation (3), Kittredge (1944,1948) found

Table 14. Coefficient correlations (r^2) for regression estimates of needle weight.

Independent Variable	Index or Coefficient of Determination					
	$Y=A+BX$	$Y=Ae^{BX}$	$Y=AX^{B}$	$Y=A+(B/X)$	$Y=1/(A+BX)$	$Y=X/(A+BX)$
DBH	.8815	.8524	.9088	.6812	.3633	.6385
Diameter - tree base	.8700	.8198	.8822	.6795	.3514	.6391
Diameter - base of contiguous crown	.8875	.7711	.8477	.7412	.2729	.4844
DBH^2	.9146	.7742	.9088	.5318	.2667	.7766
Cross-sectional area at DBH	.9146	.7743	.9089	.5313	.2669	.7770
Cross-sectional area at tree base	.8994	.7393	.8822	.5311	.2542	.7885
D^2H	.9166	.7557	.9056	.3894	.2477	.8759
Total tree height	.5729	.7383	.7588	.4731	.4660	.6603
Canopy height	.5973	.5887	.6200	.5400	.2239	.3055
Canopy volume	.8334	.7000	.8720	.1963	.2206	.9165

Table 15. Regression equations for estimation of oven-dry needle weight (g).

Y Variable ($\log_e$)	X Variable ($\log_e$)	Curve Form	Regression Constants A	Regression Constants B	r^2	R^2
Oven-dry weight needles (g)	D^2H (inches^2, ft)	Y=A+BX	-206.909	3.62298	.9166	.9166
	Canopy volume (ft^3)	Y+X/(A+BX)	2.66061E-02	1.94717E-04	.9165	.5388
	DBH^2 (inches^2)	Y=A+BX	-917.936	173.998	.9146	.9146
	Bole cross-sectional area at DBH (inches^2)	Y=A+BX	-917.745	221.548	.9146	.9146
	DBH (inches)	$Y=AX^B$	33.5602	2.8471	.9088	.9073
	D^2H (inches^2, ft)	$Y=AX^B$	1.70089	1.09785	.9056	.9195

a surprisingly small range for both constants despite a variety of species, sites, and stand ages. For oven-dry weight of leaves, the slope ranged from 1.15 to 3.15, the Y-intercept ($\log_{10}$) ranged from -0.46 to -1.16. Values of B compiled by Hozumi (1963) and cited by Tadaki (1966) for _Pinus_, _Cryptomeria_, and _Chamaecyparis_, and some broad-leaf species ranged from 1.85 to 2.13, and from 2.35 to 2.62 for coniferous trees such as _Abies_ and _Picea_. Values of B cited by Baskerville (1965a) for balsam fir, 3.21, and Ovington and Madgwick (1959b) for Scots pine, 3.63, are greater than those compiled by Hozumi (1963) for _Abies_ and _Pinus_. In comparison, the curve (3)-DBH relationship established for Lake George jack pine (Table 15) is

$$Y = 33.5602X^{2.8471}$$

$$\log_e Y = 2.8471 \log_e X - 5.815.$$

Y is oven-dry weight of needles (g); X is DBH (inches). The slope, 2.8471, is extremely close to the 2.87 value cited by Kittredge (1944,1948) for jack pine in Minnesota. Conversion to kilograms

$$\log_e Y = 2.8471 \log_e X - 3.3963$$

and $\log_{10}$ units

$$\log_{10}(X) = \log_e(X)(1/2.30258)$$

$$\log_{10} Y = 2.8471 \log_{10} X - 1.47499 \qquad \text{(SI = 40.6 ft; age = 51.3 yrs)}$$

reveals that the Y-intercept is also close to that cited by Kittredge for a slightly younger stand on a better site (Fig. 1):

$$\log_{10} Y = 2.87 \log_{10} X - 1.58 \qquad \text{(SI = 45 ft; age = 37 yrs)}$$

For both equations, Y is oven-dry weight of needles (kg), X is DBH (inches). A comparison of calculated Y values for common independent variables (Table 16), however, reveals that minor differences in the

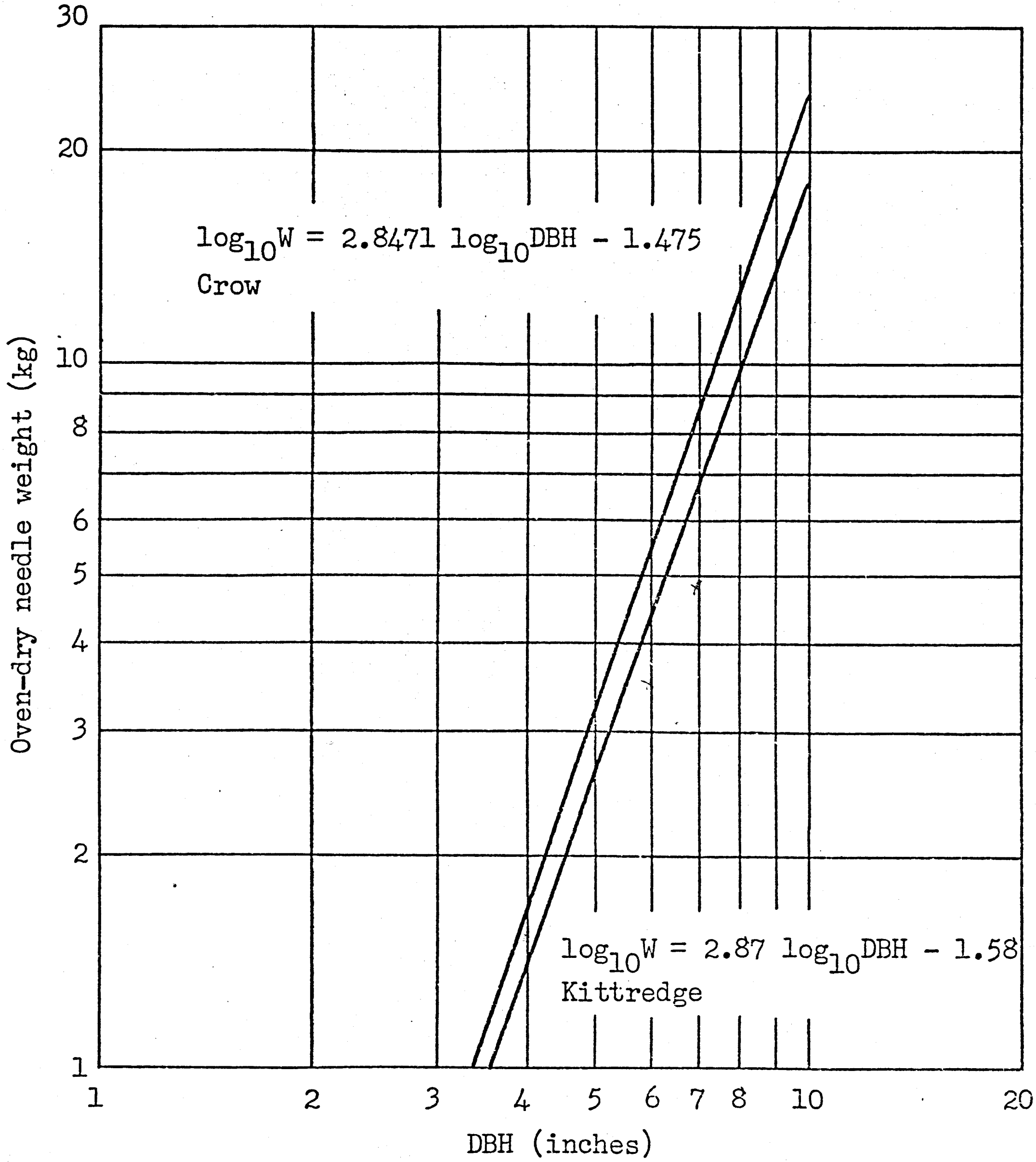

Fig. 1. Curves for estimation of needle weight for jack pine in Minnesota - Kittredge and Crow.

Table 16. Comparison of regression equations for needle weight estimation - Kittredge and Crow.

$\log_{10}W = 2.87 \log_{10}DBH - 1.58$[a,b] Kittredge (1944,1948)

DBH (inches)	$\log_{10}$	X 2.87	- 1.58	Antilog (Kg)
4	0.60206	1.72791	0.14791	1.406
5	0.69897	2.00604	0.42604	2.667
6	0.77815	2.23329	0.65329	4.500
7	0.84510	2.42543	0.84543	7.005

$\log_{10}W = 2.8471 \log_{10}DBH - 1.475$[a,c] Crow (present study)

DBH (inches)	$\log_{10}$	X 2.8471	- 1.475	Antilog (Kg)	
4	0.60206	1.71412	0.23912	1.736	1.09
5	0.69897	1.99003	0.51503	3.276	
6	0.77815	2.21547	0.74047	5.506	3.58
7	0.84510	2.40608	0.93108	8.539	4.72

[a] W = oven-dry needle weight (kg); DBH = inches

[b] SI = 45 ft; age = 37 yrs

[c] SI = 40.6 ft; age = 51.3 yrs

Y-intercept are significant since ordinate units are kg ($\log_{10}$).

Although valid application of a common equation to individuals of similar life form within a stand has been reported (Ogawa et al. 1961,1965b; Kimura 1963; Ogino et al. 1964; Tadaki 1966), application of a common form for a given species on different sites is extremely questionable since regression constants change with age or growth stage, competition, and site conditions (Ando et al. 1962; Satoo 1966; Tadaki 1966). Burger (1941) compiled data that would indicate a change in both constants with elevation for Scots pine and Norway spruce in stands of the same age. In sampling a Virginia pine stand, Madgwick (1968) noted changes in both constants with sampling date. Yearling Japanese red pine were established (Tadaki 1966) and then sampled five times during the succeeding four years to test the periodical change in the allometric relation between D^2H and oven-dry weight of needles. The regression line moved progressively rightward, a lower Y-intercept but similar slope, with time. For young Japanese cedar at various densities, the slope of the same function increased and the ordinate intersection decreased with increasing stand density (Tadaki 1966).

Although the curve (3)-DBH function for estimating leaf biomass has proven successful for numerous forest types, other independent variables may prove more accurate. As in this study, numerous authors have recommended D^2H in place of DBH (Ogawa et al. 1961,1965a,1965b; Hutnik 1964; Baskerville 1965a; Newbould 1967; Madgwick 1968). For crown components (leaves and branches) of young aspen (<u>Populus tremuloides</u> Michx.), Bella (1968) found DBH^2 to be more suitable. Ovington et al. (1967) recommended use of bole cross-sectional area at DBH as an independent variable. Shinozaki et al. (1964) and Loomis, Phares, and Crosby (1966) noted the significance of bole diameter just below the lowest living branch. According to the "pipe model theory" formulated by Shinozaki, the weight of foliage or branches is expected to be approximately proportional to (bole diameter)^2 or the cross-sectional stem area just below the lowest living branch. However, with curve (3), exactly the same fit is obtained regardless if the independent variable is diameter, diameter^2, or cross-sectional area (note r^2 values for DBH, DBH^2, and cross-sectional area at DBH for curve (3) in Table 17). For example,

$$Y_1 = 35.637X_1^{2.9814} \text{ when } X_1 = \text{DBH}$$

and $$Y_2 = 35.637X_2^{1.4907} \text{ when } X_2 = \text{DBH}^2$$

are equivalent equations since

$$(a^m)^n = a^{mn};$$

thus $Y_2 = 35.637(X_1^2)^{1.4907} = 35.637(X_2)^{2.9814}$

and $Y_1 = Y_2$.

Because π is a constant, diameter^2 should be substituted for cross-sectional area regardless of curve form.

If leaf biomass per unit area does become constant, as hypothesized, in a closed stand due to the limiting factor of light intensity, use of a hyperbolic function would avoid overestimates for larger trees. In a Cambodian rain forest, leaf biomass did reach an asymptotic value (approximately 40 kg dry weight per tree) with increasing tree size (Ogawa et al. 1965b). This leveling trend was apparent for trees larger than 40 cm in DBH. Application of the same regression form (hyperbolic curve (6) - DBH) to jack pine, however, produced a relatively low r^2 value (.6385). Although the r^2 value for hyperbolic curve (6)-canopy volume relationship (see Tables 14 and 15) was .9165, further evaluation based on R^2 and standard error of estimate indicated this relationship to be unsatisfactory compared to exponential and linear relationships:

$Y = X/(A + BX)$ X = canopy volume

$S_{y/x} = 1283.44$ g (41.43% of mean $\bar{Y}$)

$R^2 = .5388$

Because xeric site conditions do not support a closed canopy at the Lake George site, it is not surprising that all hyperbolic functions seriously underestimate needle weight for larger trees, and thus precludes their use for biomass estimates.

The variety of curve forms that are potentially valid substantiates the observation that changes in foliage weight with tree size are less regular than other tree components (Newbould 1967), or that leaf weight estimates are subject to greater error due to their sensitivity to factors such as vertical light intensity, stand density, and tree age (Ogawa et al. 1965b).

2. Live Branches

A variety of curve forms and independent variables account for more than 90% of the variation in the dependent variable (Tables 17 and 18). Based on all indicators, the best fitting function is the exponential curve (3), with DBH, DBH^2, or bole cross-sectional area at DBH as the independent variable:

$Y = AX^B$ X = DBH; DBH^2; bole cross-sectional area at DBH

Table 17. Coefficient correlations (r^2) for regression estimates of live branch weight.

Independent Variable	Index or Coefficient of Determination					
	Y=A+BX	$Y=A^{BX}$	$Y=AX^B$	Y=A+(B/X)	Y=1/(A+BX)	Y=X/(A+BX)
DBH	.8741	.9320	.9393	.6254	.5969	.8415
Diameter - tree base	.8632	.8847	.8958	.6249	.5550	.8024
Diameter - base of contiguous crown	.8977	.8746	.9156	.6948	.4910	.7271
DBH^2	.9357	.8866	.9393	.4666	.4819	.9160
Cross-sectional area at DBH	.9357	.8867	.9393	.4662	.4820	.9161
Cross-sectional area at tree base	.9171	.8384	.8958	.4659	.4446	.8851
D^2H	.9168	.8628	.9147	.3259	.4571	.9316
Total tree height	.4886	.7097	.7066	.3970	.6433	.7910
Canopy height	.4810	.5628	.5903	.4347	.3613	.4476
Canopy volume	.8686	.8220	.8178	.1430	.4198	.8138

Table 18. Regression equations for estimation of live branch weight (g).

Y Variable ($\log_e$)	X Variable ($\log_e$)	Curve Form	Regression Constants A	B	r^2	R^2
Oven-dry weight live branches (g)	DBH (inches)	$Y=AX^B$	35.6374	2.98144	.9393	.9552
	DBH^2 ($inches^2$)	$Y=AX^B$	35.643	1.49067	.9393	.9552
	Bole cross-sectional area at DBH ($inches^2$)	$Y=AX^B$	51.1589	1.49027	.9393	.9552
	DBH^2 ($inches^2$)	$Y=A+BX$	-2339.51	284.286	.9357	.9357
	D^2H ($inches^2$, ft)	$Y=X/(A+BX)$	.258707	-1.26593E-05	.9316	.8386
	DBH (inches)	$Y=A^{BX}$	153.441	0.65361	.9320	.9391

$S_{y/x}$ = 670.862 g (15.89% of mean Y)

R^2 = .9552

r^2 = .9393

Numerous other curve forms had excellent correlation coefficients, but proved less satisfactory. For example, the linear equation (1)-DBH^2 function

$Y = A + BX$ $\qquad$ $X = DBH^2$

$S_{y/x}$ = 810.828 g (19.21% of mean Y)

R^2 = .9357

r^2 = .9357

underestimates the oven-dry weight of live branches for nine of the 10 smallest harvested trees; a negative estimate is also possible for extremely small values of the independent variable:

Y-Actual	Y-Calculated
445.5 g	-835.6 g
1307.4	51.3
1126.9	571.6
954.1	756.4
1353.0	1143.0
1842.4	1143.0
2408.7	1552.4
1716.7	1765.6
2399.2	1981.6
2238.9	1984.5

The hyperbolic curve (6)-D^2H function

$Y = X/(A + BX)$ $\qquad$ $X = D^2H$

$S_{y/x}$ = 1189.39 g (28.18% of mean Y)

R^2 = .8386

r^2 = .9316

consistently underestimates oven-dry weight of branches for large trees. The comparison of calculated values to actual values of Y is as follows:

Y-Actual	Y-Calculated
10015.1 g	8257.6 g
12546.3	8682.1
7781.0	6230.4
10198.8	7354.9
8545.8	7255.3
13678.8	9625.5
5553.7	6684.0

Exponential curve form

$$Y = Ae^{BX} \qquad (2)$$

with its linear transformation

$$\log Y = \log A + BX, \qquad (2)$$

rarely cited in the literature and less satisfactory than exponential curve (3) in this study, did have a high coefficient of determination for live branch weight when used with DBH:

$Y = Ae^{BX}$ $\qquad$ $X = DBH$

$S_{y/x} = 788.266$ g (18.67% of mean Y)

$R^2 = .9391$

$r^2 = .9320$

However, the fit is less reliable than the exponential curve (3)-D^2H function.

Correlation coefficients for live branch weight functions are generally higher than those recorded for needle weight. Branch weight for individual trees can be predicted with considerable accuracy from bole measurements and the estimation of biomass on an individual branch basis as recommended by Newbould (1967) is not necessary for the coniferous jack pine. Comparisons of relationships are fewer than those published for needle and leaf components. For diverse stands ranging from savanna to dry monsoon and tropical rain forests in Thailand and Cambodia, the constant B in the curve (3)-D^2H function was always close to unity, 0.961 to 1.279 (Ogawa et al. 1965b; Hozumi et al. 1969). The constant B for the same relationship with jack pine equalled 1.137, again close to unity.

3. Cones and Dead Branches

Despite many significant ($P < .01$) relationships for estimating the oven-dry weight of cones and dead branches, correlations between variables for all curve types are lower than other components (Tables 19, 20 and 21). Neither cones nor dead branches function as mechanical support or have a photosynthetic capacity, thus the lower correlation between mass and a measurable parameter are expected. Despite large potential errors in regression estimates of cone and dead branch oven-dry weight, the small proportionate weight of these components has little effect on total biomass estimates.

Although the change of dead branch weight with tree size is rather variable, an exponential trend is evident. The allometric regression curve (2) with DBH best describes the trend (Table 21):

$Y = Ae^{BX}$ $\qquad$ $X = DBH$

$S_{y/x} = 639.872$ g (49.59% of mean Y)

F-ratio = 40.84(**)

$r^2 = .5854$

$r = .7651$

No such exponential trend is evident for cones. The regression of cone weight is best described with the linear curve and cross-sectional area at the base of the tree:

$Y = A + BX$ $\qquad$ X = cross-sectional area of tree base

Table 19. Coefficient correlations (r^2) for regression estimates of dead branch weight.

Independent Variable	Index or Coefficient of Determination					
	$Y=A+BX$	$Y=A^{BX}$	$Y=AX^B$	$Y=A+(B/X)$	$Y=1/(A+BX)$	$Y=X/(A+BX)$
DBH	.5118	.5854	.5796	.4004	.5107	.5278
Diameter - tree base	.4743	.5483	.5583	.3946	.4810	.5149
Diameter - base of contiguous crown	.4159	.4497	.4580	.3499	.3749	.4025
DBH^2	.5224	.5589	.5796	.3100	.4594	.4734
Cross-sectional area at tree base	.4673	.5075	.5583	.3112	.4230	.4650
D^2H	.4686	.5170	.5307	.2076	.4291	.3530
Total tree height	.2404	.3726	.3616	.2139	.3965	.3729
Canopy height	.1387	.2198	.2354	.1579	.2426	.2511
Canopy volume	.5084	.5406	.5283	.1117	.4317	.2826

Table 20. Coefficient correlations (r^2) for regression estimates of cone weight.

Independent Variable	Index or Coefficient of Determination					
	$Y=A+BX$	$Y=A^{BX}$	$Y=AX^B$	$Y=A+(B/X)$	$Y=1/(A+BX)$	$Y=X/(A+BX)$
DBH	.3861	.2750	.2884	.3074	.0236	.0418
Diameter - tree base	.4229	.2859	.2920	.3247	.0251	.0386
Diameter - base of contiguous crown	.3853	.2642	.2791	.3300	.0237	.0328
DBH^2	.3964	.2535	.2884	.2438	.0171	.0492
Cross-sectional area at tree base	.4412	.2346	.2919	.2518	.0204	.0444
D^2H	.3941	.2554	.2941	.1828	.0195	.0329
Total tree height	.2567	.2642	.2642	.2213	.0527	.0580
Canopy height	.2296	.2264	.2257	.2147	.0578	.0473

Table 21. Regression equations for estimation of dead branch and cone weight (g).

Y Variable ($\log_e$)	X Variable ($\log_e$)	Curve Form	Regression Constants A	Regression Constants B	r^2	R^2
Oven-dry weight dead branches (g)	DBH (inches)	$Y=A^{BX}$	124.972	.454517	.5854	.4921
Oven-dry weight cones (g)	Cross-sectional area at base of tree (inches^2)	$Y=A+BX$	-90.9543	13.1087	.4412	.4412

$S_{y/x}$ = 252.044 g (65.68% of mean Y)

F-ratio = 25.53(**)

r^2 = .4412

r = .6642

4. Bole (wob) and Bole Bark

Coefficients of determination recorded for estimates of bole (wob) weight are extremely high (Tables 22 and 23). Oven-dry weight of bolewood, by far the largest fraction of forest biomass, can be accurately estimated with any of several independent variables and curve forms. Comparison of standard error of estimate and R^2 values for the exponential curve (3)-DBH function, the exponential curve (3)-D^2H function, and the linear curve (1)-DBH function reveals little difference in reliability of estimate among the relationships:

$Y = AX^B$ | X = DBH; DBH^2; cross-sectional area at DBH

$S_{y/x}$ = 3.1411 kg (12.31% of mean Y)

R^2 = .9495

$Y = A + BX$ | X = DBH^2

$S_{y/x}$ = 3.1910 kg (12.51% of mean Y)

R^2 = .9479

$Y = AX^B$ | X = D^2H

$S_{y/x}$ = 3.1996 kg (12.54% of mean Y)

R^2 = .9412

Despite a r^2 of .9825, the hyperbolic curve (3)-D^2 H function is unreliable. Significant underestimates of bole weight for larger trees are reflected in R^2 and standard error of estimate values:

Table 22. Coefficient correlations (r^2) for regression estimates of bole (wob) weight.

Independent Variable	Index or Coefficient of Determination					
	$Y=A+BX$	$Y=A^{BX}$	$Y=AX^B$	$Y=A+(B/X)$	$Y=1/(A+BX)$	$Y=X/(A+BX)$
DBH	.9190	.9272	.9616	.7232	.6426	.8948
DBH^2	.9479	.8611	.9616	.5708	.5212	.9648
D^2H	.9520	.8591	.9744	.4314	.5076	.9825

Table 23. Regression equations for estimation of bole (wob) weight (kg).

Y Variable ($\log_e$)	X Variable ($\log_e$)	Curve Form	Regression Constants		r^2	R^2
			A	B		
Oven-dry weight bole (wob) (kg)	DBH^2 (inches^2)	Y=A+BX	-3.21594	1.25164	.9479	.9479
	DBH (inches)	$Y=AX^B$	.696036	2.286	.9616	.9495
	D^2H (inches^2, ft)	$Y=AX^B$	6.04127E-02	.889101	.9744	.9412
	D^2H (inches^2, ft)	Y=X/(A+BX)	.982499	27.193	.9825	.8630

$Y = X/(A + BX)$ $\quad X = D^2H$

$S_{y/x} = 4.8363$ kg (18.95% of mean Y)

$R^2 = .8630$

The value of B in the bole weight-DBH-curve (3) relationship for non-senile stands is always greater than 2.0 (Attiwill 1966); 2.7 (Kuroiwa 1959) and 2.5 (Baskerville 1959a) for Abies; 2.6 (Ovington and Madgwick 1959a) and 2.5 (Baskerville 1965a) for Betula; 2.4 (Rutter 1957), 2.5 (Ovington 1957), and 2.6 (Ovington and Madgwick 1959b) for Scots pine. For the Lake George jack pine, B equals 2.3.

Although the curve (3)-DBH allometry is slightly superior in fit in this study, use of D^2H may be more desirable. Ogawa et al. (1961, 1965b) warn of serious errors if the curve (3)-DBH allometry is used to estimate biomass beyond the actual observed limit of stem diameters. The logarithmic transformation of the stem weight-DBH curve becomes slightly hyperbolic at larger diameters, thus approximations for larger trees based on a straight line function result in overestimates. Use of D^2H, a variable supposedly proportional to stem volume, avoids this potential hazard. The linearity between log stem weight and log D^2H has proven to hold over a greater range of tree sizes as compared with the log stem weight - log DBH regression (Ogawa et al. 1961). Ogawa et al. (1965b) noted another advantage of the D^2H variable. Ogawa reported "no appreciable inter-stand difference" among three forest types (savanna, dry monsoon, and tropical rain forest) in Thailand with respect to the curve (3)-D^2H regression form when used to estimate stem weight. In contrast, curve (3)-DBH functions for stem weight estimates were significantly different.

Correlations between tree parameters or between tree components are also valuable. In contrast to the ease of measuring DBH, accurate measurements of total tree height for the D^2H parameter are difficult in a dense, closed forest. A more accurate determination of tree height in such cases can be made from a reliable tree height-DBH curve (Ogawa et al. 1961,1965b; Hozumi et al. 1969). Based on 74 sample trees (50 species) in a Thailand rain forest (Kira et al. 1964), weight of stem, branches, and roots was most closely correlated to D^2H in the exponential equation

$$Y = AX^B, \tag{3}$$

but leaf weight was best correlated to stem weight in the hyperbolic equation

$$Y = X/(A + BX). \tag{6}$$

For estimates of bole bark, the hyperbolic function again appears superior, but further evaluation indicates the exponential function (3)-D^2H allometry to be slightly superior in fit than linear or hyperbolic functions (Tables 24 and 25):

$Y = AX^B$

$X = D^2H$

$S_{y/x} = 685.414$ g (15.41% of mean Y)

$R^2 = .8906$

$r^2 = .9264$

$Y = A + BX$

$X = DBH$

$S_{y/x} = 701.398$ g (15.77% of mean Y)

$R^2 = .8858$

$r^2 = .8858$

Table 24. Coefficient correlations (r^2) for regression estimates of bole bark weight.

Independent Variable	Index or Coefficient of Determination					
	$Y=A+BX$	$Y=A^{BX}$	$Y=AX^B$	$Y=A+(B/X)$	$Y=1/(A+BX)$	$Y=X/(A+BX)$
DBH	.8858	.8012	.9188	.7462	.6517	.8879
DBH^2	.8815	.8003	.9188	.6079	.5386	.9458
D^2H	.8821	.7934	.9264	.4687	.5226	.9437

Table 25. Regression equations for estimation of bole bark weight (g).

Y Variable ($\log_e$)	X Variable ($\log_e$)	Curve Form	Regression Constants A	B	r^2	R^2
Oven-dry weight bole bark (g)	DBH^2 ($inches^2$)	Y=X/(A+BX)	5.5894E-03	-1.7169E-05	.9458	.8284
	D^2H ($inches^2$,ft)	$Y=AX^B$	24.0345	.768794	.9264	.8906
	DBH (inches)	Y=A+BX	-3772.14	1756.4	.8858	.8858
	D^2H ($inches^2$,ft)	Y=X/(A+BX)	.123603	8.7527E-05	.9437	.8112

$Y = X/(A + BX)$ — $X = DBH^2$

$S_{y/x} = 841.387$ g (18.92% of mean Y)

$R^2 = .8284$

$r^2 = .9458$

$Y = X/(A + BX)$ — $X = D^2H$

$S_{y/x} = 856.613$ g (19.31% of mean Y)

$R^2 = .8115$

$r^2 = .9437$

The hyperbolic curve (6)-D^2H allometry is totally unacceptable with 17 of the largest 20 harvested trees underestimated using this function.

5. Roots

The pattern of fit for roots is similar to other components (Tables 26 and 27). Little difference is found in closeness of fit between the linear and exponential forms, with the exponential-DBH^2 function only slightly superior to the linear curve (1)-DBH^2 function.

$Y = AX^B$ — X = DBH; DBH^2; cross-sectional area at DBH

$S_{y/x} = 1186.48$ g (16.56% of mean Y)

$R^2 = .9170$

$r^2 = .9361$

$Y = A + BX$ — $X = DBH^2$

$S_{y/x} = 1197.49$ g (16.71% of mean Y)

$R^2 = .9159$

$r^2 = .9159$

Despite a high r^2 value, the hyperbolic function is unacceptable.

Table 26. Coefficient correlations (r^2) for regression estimates of root weight.

Independent Variable	Index or Coefficient of Determination					
	$Y=A+BX$	$Y=A^{BX}$	$Y=AX^{B}$	$Y=A+(B/X)$	$Y=1/(A+BX)$	$Y=X/(A+BX)$
DBH	.8792	.9240	.9361	.7306	.7674	.9027
DBH^2	.9159	.8852	.9361	.6321	.6762	.9250
Diameter - tree base	.8876	.8869	.9099	.7896	.7241	.8599
D^2H	.9040	.8557	.9369	.5653	.6359	.9363

Table 27. Regression equations for estimation of root weight (g).

Y Variable ($\log_e$)	X Variable ($\log_e$)	Curve Form	Regression Constants A	Regression Constants B	r^2	R^2
Oven-dry weight roots (g)	D^2H (inches^2,ft)	$Y=AX^B$	24.6412	.83636	.9370	.8959
	DBH (inches)	$Y=AX^B$	243.411	2.16039	.9361	.9170
	DBH^2 (inches^2)	$Y=A+BX$	-825.956	355.923	.9159	.9159

6. Total Tree

Again the exponential curve (3)-DBH^2 function proved only slightly superior in fit to the linear curve (1)-DBH^2 function for estimating the oven-dry weight of the complete tree (Tables 28 and 29).

$Y = AX^B$

X = DBH; DBH^2; cross-sectional area at DBH

$S_{y/x} = 3.8208$ kg (8.64% of mean Y)

$R^2 = .9784$

$r^2 = .9748$

$Y = A + BX$

$X = DBH^2$

$S_{y/x} = 3.9796$ kg (9.99% of mean Y)

$R^2 = .9766$

$r^2 = .9766$

Use of the exponential curve (3)-D^2H function did not improve the accuracy of the estimate ($S_{y/x} = 5.3368$ kg). Regression estimates of total tree weight, above and below-ground components, are more accurate than estimates for any of the individual components.

The slight superiority in fit of the exponential curve (3) compared to the linear curve has been reported for needles, bole (wob), bole bark, and roots, and is repeated for the total tree. The relatively small size range represented in an even-aged stand no doubt contributes to the lack of strong exponential trends. The linear function is a convenient regression form that can be applied to most components in this study with only a slight reduction in reliability of the estimate.

Table 28. Coefficient correlations (r^2) for regression estimates of total tree weight.

Independent Variable	Index or Coefficient of Determination					
	$Y=A+BX$	$Y=A^{BX}$	$Y=AX^B$	$Y=A+(B/X)$	$Y=1/(A+BX)$	$Y=X/(A+BX)$
DBH	.9533	.9577	.9748	.8260	.8133	.9425
DBH^2	.9766	.9148	.9748	.7334	.7239	.9637
D^2H	.9622	.9155	.9772	.6543	.7270	.9719

Table 29. Regression equations for estimation of total tree weight (kg).

Y Variable ($\log_e$)	X Variable ($\log_e$)	Curve Form	Regression Constants A	Regression Constants B	r^2	R^2
Oven-dry weight total tree (kg)	DBH (inches)	$Y=AX^B$	1.26471	2.27266	.9748	.9784
	DBH^2 (inches^2)	$Y=A+BX$	-5.9911	2.23848	.9766	.9766

E. Multiple Regressions

A test of successive independent variables as outlined by Freese (1962) was utilized to determine if use of a second or third independent variable resulted in a significant reduction of residuals when fitted after X_1. The procedure was to apply an analysis of variance to each relationship and determine the following ratio:

F = mean square difference for testing hypothesis/mean square residual about maximum model.

If a second independent variable is being tested, the null hypothesis would be $B_2 = 0$.

Results indicate little advantage in using multiple regressions in place of simple allometric functions. DBH, DBH^2, D^2H are independent variables which maximize the fit of simple allometric functions. The test of successive terms using a combination of these variables rarely indicated a significant reduction in residuals. For example, with Y equal to oven-dry weight (kg) of total tree, there was no significant difference ($P < .01$) between

$$Y = B_0 + B_1(DBH) + B_2(DBH^2) + B_3(D^2H) \qquad r^2 = .9782 \qquad \text{(a)}$$

and

$$Y = B_0 + B_1(DBH) + B_2(DBH^2) \qquad r^2 = .9782$$

$$Y = B_0 + B_1(DBH) + B_2(D^2H) \qquad r^2 = .9641$$

$$Y = B_0 + B_1(DBH^2) \qquad r^2 = .9766$$

$$Y = B_0 + B_1(D^2H) \qquad r^2 = .9622$$

There was, however, a significant difference ($F = 9.45$ (**); $N = 20$; $P > .01$) between function (a) and

$$Y = B_0 + B_1(DBH) \qquad r^2 = .9533$$

A similar analysis with the model

$$\log_e Y = B_0 + \log_e X_n$$

indicated no significant difference ($P < .01$) for the same combinations of independent variables. The lack of additional confidence from combinations of DBH, DBH^2, and D^2H can be attributed to the close correlations among these variables (Table 30).

For estimates of total tree weight, inclusion of total height as a variable did not make a significant reduction in the residuals when fitted after DBH. The form

$$\log_e Y = B_0 + B_1 \log_e(\text{DBH}) + B_2 \log_e(\text{total tree height}) \qquad r^2 = .9786,$$

also used by Young et al. (1964) to estimate the biomass of seven tree species in Maine and by Dyer (1967) to estimate the biomass of northern white cedar (*Thuja occidentalis* L.), was not significantly different from

$$\log_e Y = B_0 + B_1 \log_e(\text{DBH}) \qquad r^2 = .9748$$

$$(F = 3.07;\ P < .01;\ N = 20)$$

for jack pine. The lower correlations between tree height and other independent variables (Table 30) are a product of the rather uniform vertical extension of a mature, even-aged stand.

Attempts to improve coefficients for poorly correlated tree components, cones and dead branches, with multiple regressions also proved ineffectual. For example, combination of DBH with a non-diameter parameter, canopy volume, did not significantly reduce the residuals for estimates of dead branch weight:

$$\log_e Y = B_0 + B_1 \log_e(\text{DBH}) \qquad r^2 = .5796$$

$$\log_e Y = B_0 + B_1 \log_e(\text{DBH}) + B_2 \log_e(\text{canopy volume}) \qquad r^2 = .5902$$

$$(F = 0.96;\ P < .01;\ N = 40).$$

Table 30. Simple linear correlation coefficients (r) between independent variables.

	DBH	DBH^2	D^2H	Diameter Tree Base	Total Height	Canopy Volume
DBH	1.0					
DBH^2	.9898	1.0				
D^2H	.9826	.9938	1.0			
Diameter Tree Base	.9751	.9691	.9588	1.0		
Total Height	.8605	.8086	.8410	.8576	1.0	
Canopy Volume	.9269	.9391	.9363	.9203	.7484	1.0

F. Evaluation of Stand Estimate Techniques

An estimate of oven-dry weight for each component was derived from that curve form and independent variable giving the strongest correlation or closest relationship. As cited in Section D, the strongest correlations were obtained with the following equations:

needles	$Y = AX^B$	$X = D^2H$
live branches	$Y = AX^B$	$X = DBH; DBH^2$; or cross-sectional area at DBH
cones	$Y = A + BX$	$X =$ cross-sectional area at base of tree
dead branches	$Y = Ae^{BX}$	$X = DBH$
bole (wob)	$Y = AX^B$	$X = DBH; DBH^2$; or cross-sectional area at DBH
bole bark	$Y = AX^B$	$X = D^2H$
roots	$Y = AX^B$	$X = DBH; DBH^2$; or cross-sectional area at DBH

Total above-ground and total tree estimates are a summation of individual components. Summation of estimates for all 180 trees within the study plots provides the stand estimate to which the "mean tree" estimates are compared (Tables 31 and 32).

Trees with mean stand dimensions were then selected, the biomass calculated for each component with the above equations, and the weight multiplied by the number of trees per unit area. Mean stand dimensions of primary importance are:

mean stand height - 38.11 ft

mean stand DBH - 4.77 inches

basal area (BA) - 0.1308 ft^2

bole (wob) volume - 5.0203 ft^3

Table 31. Comparison of "mean tree" estimates to every-tree summation.

Base of Estimate	Needles	Dead Branches	Live Branches	Cones	Bole (wob)	Bole Bark	Roots
			Kilograms per Hectare				
Every-tree summation	4840.3	1854.5	6492.2	596.2	39663.8	6814.9	11271.7
Tree of mean height	3539.2 (-26.9)[a]	1368.9 (-26.2)	4378.8 (-32.6)	458.3 (-23.1)	30520.9 (-23.1)	5698.5 (-16.4)	8860.9 (-21.4)
Tree of mean height and mean DBH	4284.3 (-11.5)	1641.9 (-11.5)	5675.7 (-12.6)	567.9 (-4.7)	37237.7 (-6.1)	6514.2 (-4.4)	10693.5 (-5.1)
Tree of mean DBH	4408.2 (-8.9)	1641.9 (-11.5)	5675.7 (-12.6)	567.9 (-4.7)	37237.7 (-6.1)	6645.6 (-2.5)	10693.5 (-5.1)
Tree of mean BA	4612.4 (-4.7)	1718.2 (-7.3)	6035.5 (-7.0)	596.8 (+0.1)	39035.1 (-1.6)	6859.7 (+0.7)	11180.6 (-0.8)
Tree of mean bole volume	4957.4 (+2.4)	1798.1 (-3.0)	6410.2 (-1.3)	626.3 (+5.0)	40880.1 (+3.1)	7215.2 (+5.9)	11679.4 (+3.7)

[a]Percent deviation from every-tree summation.

Table 32. Comparison of "mean tree" estimates to every-tree summation - above-ground components and total tree.

Base of Estimate	Total Above-Ground	Total Tree
	Kilograms per Hectare	
Every-tree summation	60262.0	71533.7
Tree of mean height	45964.7 (-23.7)[a]	54825.6 (-23.4)
Tree of mean height and mean DBH	55921.7 (-7.2)	66615.2 (-6.9)
Tree of mean DBH	56177.0 (-6.8)	66870.5 (-6.5)
Tree of mean BA	58857.7 (-2.3)	70038.3 (-2.1)
Tree of mean bole volume	61887.4 (+2.7)	73566.8 (+2.8)

[a]Percent deviation from every-tree summation.

Total tree height was measured to the nearest ft and DBH to the nearest 0.1 inch, thus the significant stand averages are 38 ft for height and 4.8 inches for DBH. For all mean stand dimensions, more than a single tree met the qualifications. For example, eight trees, ranging in DBH from 3.8 to 4.8 inches, had a total height of 38 feet. The tree closest to the median dimension, in this case 4.4 inches DBH, was selected. The dimensions of selected trees are presented in Table 33.

When based on a tree of mean total height, total biomass is underestimated by 23.4% and individual components by as much as 32.5% (Tables 31 and 32). However, successive improvements are noted with estimates based on a tree of mean total height X mean DBH, mean DBH, and mean BA. Based on the tree of mean BA, total tree biomass is underestimated by only 2.1%, with a maximum deviation of -7.3% for dead branches. Estimates based on the tree of mean bole (wob) volume are generally greater than the every-tree summation. The total tree biomass is overestimated by 2.8%, with a maximum deviation of +5.0% for cones.

An interesting comparison can be made to a similar analysis with balsam fir (Table 3) by Baskerville (1965b); deviations from the best estimate are substantially greater than for jack pine. Estimates by Baskerville (1965b) of total tree biomass for the balsam fir stand based on the tree of mean height deviated -50.2%, tree of mean diameter by -29.8%, tree of mean BA by -12.2%, and tree of mean bole volume by +0.1% from the every-tree summation. Deviations for jack pine are also considerably less than those reported by Ogawa et al.

Table 33. Comparison of dimensions for "mean trees" to mean stand DBH and tree height.

Parameter	Tree Number	DBH (inches)	Total Height (ft)
Tree of mean total height	B2	4.4	38
Tree of mean height and DBH	C2	4.8	38
Tree of mean DBH	B22	4.8	39
Tree of mean BA	B38	4.9	39
Tree of mean bole (wob) volume	B5	5.0	40

Mean stand DBH = 4.77 inches

Mean stand total height = 38.11 ft

(1961) and Attiwill (1966). Estimates by Ogawa based on the tree of mean DBH deviated as much as -60% from the actual standing crop. For crown weight estimates of Eucalyptus by Attiwill, underestimates of 30-40% occurred when based on the tree of mean DBH and -18% when based on the tree of mean BA. Because of the diversity of tree size in an all-aged stand, Baskerville (1965b) recommended use of a stand table approach, in which estimates are based on the weight of a mean tree within each DBH class multiplied by the frequency within the class. This approach underestimated total tree biomass for the balsam fir stand by 1.0%, with a maximum component error of only 2.9% (roots).

The percent deviations for stand biomass estimates based on a tree of mean BA reported by Satoo (1967b) for a Japanese red pine stand are remarkably similar to those for the Lake George jack pine:

	Japanese red pine (Satoo 1967b)	Lake George jack pine
foliage	-3.5%	-4.7%
branches	-6.9%	-7.0% (live branches)
stemwood	+3.8%	-1.6%
total above-ground	+5.6%	-2.3%
total tree	-0.7%	-2.1%

Although the advantage of a stand table approach for biomass estimates in a heterogeneous, all-aged stand is obvious, estimates based on a single tree of mean BA did prove satisfactory for these homogeneous, even-aged pine stands. For jack pine, bole and root components, comprising 70% of total tree biomass, deviate approximately 1% from the every-tree summation. The 7% deviation for dead branches, a minor component, is tolerable; however, a similar deviation for live branches may not be tolerable, depending on study requirements. Minimal deviations for canopy components are obtained by using the tree of mean bole volume as the basis of estimate.

With estimates based on the mean of linear measurements (height and diameter), deviations from the best estimate are reduced when estimates are based on individuals at ± one standard deviation from a stand mean. For example, when stand estimates are based on diameters at ± one standard deviation from mean stand DBH (3.654 inches and 5.885 inches), deviations for all components are 1% and less. Because the relationship between biomass and a parameter such as DBH is generally exponential, stand estimates based on a single tree of mean stand DBH will always underestimate stand biomass. Use of the ± SD estimate allows a weighted estimate necessary for an allometric function.

Because mean tree estimates in Table 31 and 32 are regression estimates, not actual weights determined from a harvest sample, one source of error has been ignored - variation of individual trees around the regression line. With the elimination of this error, the trends among mean tree estimates are more evident, and in most cases the regression estimates approximate a median estimate.

Except for dead branches and cones, the most reliable regressions were obtained with the equation

$$Y = AX^B \qquad (3)$$

and the independent variables of DBH, DBH^2, and D^2H. Recognizing that DBH^2 is a factor of BA, a great deal of information is available regarding the suitability of "mean tree" estimates from the form of equation (3), and specifically the equation constant B. If oven-dry weight (Y) is expressed as a function of DBH, the equations for the Lake George jack pine are:

needles	$Y = AX^{2.8471}$	$X = DBH$
live branches	$Y = AX^{2.9814}$	
dead branches	$Y = AX^{2.0551}$	
cones	$Y = AX^{2.4593}$	
bole (wob)	$Y = AX^{2.2860}$	
bole bark	$Y = AX^{1.9816}$	
tree roots	$Y = AX^{2.1604}$	
total tree	$Y = AX^{2.2727}$	

As given by Kuroiwa (1959) and Attiwill (1966), the DBH of the tree of mean dry weight within a stand is

$$\left(\frac{\sum_{i=1}^{i=n'} DBH^{B}}{n'} \right)^{1/B}$$

where n' is the number of trees per unit area and B is the regression constant. Thus, the tree of mean leaf dry weight

$$\left(\frac{\sum_{i=1}^{i=n'} DBH^{2.8471}}{n'} \right)^{1/2.8471}$$

will have a greater DBH than either the tree of mean BA

$$\left(\frac{\sum_{i=1}^{i=n'} DBH^{2.0}}{n'} \right)^{1/2.0}$$

or the tree of mean DBH

$$\left(\frac{\sum_{i=1}^{i=n'} \text{DBH}}{n'} \right)$$

Because it is safe to assume in this study that larger trees have greater needle biomass, underestimates of needle weight will occur if based on the tree of mean DBH or even BA. As is recorded in Table 31, and is obvious from the above values of B, underestimates of biomass occur for all components if the tree of mean stand DBH is the basis of estimate. The value of B for many components is slightly greater than 2.0 and thus the oven-dry weight is approximately proportional to DBH^2 or BA; note in Table 34 that B approximates 1.0 when $X = \text{DBH}^2$ for all components except needles and live branches. Therefore, estimates based on the tree of mean BA should be and are much more satisfactory, although the general pattern of underestimates still persists. For canopy components, B approaches unity when D^2H, the approximation of bole volume, is the independent variable (Table 34). The tree of mean bole volume does provide the superior estimate for needle and branch weight.

Calculation of DBH for the mean tree of each component allows an interesting comparison to the diameters of selected trees and the mean stand diameter in Table 33:

needles	4.997 inches DBH
live branches	5.014
cones	4.948
dead branches	4.898
bole (wob)	4.927

Table 34. Exponential equations ($Y=AX^B$) for estimates of oven-dry weight.

Component	Equation Form[a]	Independent Variable
Needles	$Y=33.5602\ X^{2.8471}$	X=DBH
	$Y=33.5671\ X^{1.42314}$	$X=DBH^2$
	$Y=1.70089\ X^{1.09785}$	$X=D^2H$
Live branches	$Y=35.6374\ X^{2.98144}$	X=DBH
	$Y=35.643\ X^{1.49067}$	$X=DBH^2$
	$Y=1.71117\ X^{1.13677}$	$X=D^2H$
Dead branches	$Y=46.5483\ X^{2.05505}$	X=DBH
	$Y=46.5604\ X^{1.02723}$	$X=DBH^2$
	$Y=6.27697\ X^{0.76937}$	$X=D^2H$
Cones	$Y=5.87994\ X^{2.4593}$	X=DBH
	$Y=5.88126\ X^{1.22958}$	$X=DBH^2$
	$Y=0.41403\ X^{0.96003}$	$X=D^2H$
Bole (wob)	$Y=0.69604\ X^{2.286}$	X=DBH
	$Y=0.69604\ X^{1.143}$	$X=DBH^2$
	$Y=0.060413\ X^{0.8891}$	$X=D^2H$
Bole bark	$Y=197.458\ X^{1.98158}$	X=DBH
	$Y=197.477\ X^{0.99077}$	$X=DBH^2$
	$Y=24.0345\ X^{0.76879}$	$X=D^2H$

Table 34, continued

Component	Equation Form[a]	Independent Variable
Roots	$Y=243.411\ X^{2.16039}$	X=DBH
	$Y=243.417\ X^{1.08019}$	$X=DBH^2$
	$Y=24.6412\ X^{0.83636}$	$X=D^2H$
Total tree	$Y=1.26471\ X^{2.27266}$	X=DBH
	$Y=1.26471\ X^{1.26471}$	$X=DBH^2$
	$Y=0.10579\ X^{0.89245}$	$X=D^2H$

[a]Y = oven-dry weight in g (canopy, bole bark, roots) or kg (bolewood, total tree).

bole bark	4.888
roots	4.911
total tree	4.925

Although stand estimates for tree components are based on the most precise method, a summation of regression estimates for all 180 trees within the study plots, this technique does not indicate the reliability of these sample based estimates. Confidence intervals were constructed from bole and root estimates based on the tree of mean BA and canopy estimates based on the tree of mean bole volume to provide such information. The calculated confidence intervals for the mean of the estimates included the finite population correction

$$S_{\hat{y}_M}^2 = \mathrm{MSE}\left(1/n + \frac{(x-\bar{x})^2}{\sum(x-\bar{x})^2}\right)$$

$$\hat{Y}_i \pm (t_{n-2})(S_{\hat{y}_M})\left(\sqrt{\frac{N-n}{N}}\right)$$

The 95% intervals for mean estimates in kg/ha are as follows:

needles	4957 ± 238
dead branches	1798 ± 285
live branches	6410 ± 295
cones	626 ± 110
bole (wob)	39,035 ± 1342
bole bark	6860 ± 287
roots	11,181 ± 508

G. Distribution of Organic Matter

1. Arboreal Layer

Relative distribution of biomass among tree components can be based on absolute weights of the 20 trees selected for complete harvest in proportion to the frequency within each crown class

needles - 6.78% of total oven-dry weight

dead branches - 2.58%

live branches - 9.05%

cones - 0.83%

canopy - 19.25%

bole (wob) - 55.28%

bole bark - 9.76%

total above-ground - 84.29%

roots - 15.71%

total tree - 100%

or based on the regression estimates of the 180 trees

needles - 6.77% of total oven-dry weight

dead branches - 2.59%

live branches - 9.07%

cones - 0.83%

canopy - 19.26%

bole (wob) - 55.45%

bole bark - 9.53%

total above-ground - 84.24%

roots - 15.76%

total tree - 100%

The closeness between the distribution based on absolute weights and regression estimates is another indication that the selected curves do adequately represent the trends between variables.

Based on the summation of regression estimates for the 180 trees, foliage represents 43% of live canopy weight (needle and live branch), substantially greater than the 21% reported for jack pine by Brown (1965). Needles represent 35% of total canopy weight (needles, live branch, dead branch, cones), far lower than the proportion, approximately 50%, cited by Burger (1937,1950,1951,1952) for most conifers.

Roots account for 16% of total tree biomass, which is within the range, 14% to 34%, cited for 14 upland, coniferous communities by Rodin and Bazilevich (1967). The root/total tree percentage for jack pine is comparable to the 17.1% for a Japanese red pine stand (Satoo 1967b), but is much lower than the 25% for a 55 year-old Scots pine plantation (Ovington 1956). Less comparable but of interest is the ratio of root/shoot volume, .20-.25, cited for pine in older German literature (Erteld and Hengst 1966). In terms of standing crop, the root/above-ground ratio for Lake George jack pine is .187. In terms of annual increment, Bray (1963) found the root/above-ground ratios for temperate forests to range from .15 to .33 with a mean of .21.

Bark weight is slightly less than 10% of total biomass; although considerably less important than bole or root biomass, the mineral accumulation in bark is very high (Cole et al. 1967) and thus should be considered in mineral cycling studies.

To test for changes in relative distribution of component weight with tree size, percentages were calculated for each crown class among the 20 trees completely harvested (Table 35). Trends were most evident for live branches, bole bark, and bolewood. Average percent of live branches increased from 6.68% of total oven-dry weight for suppressed trees to 10.68% for dominant trees, bole bark decreased from 11.96% (suppressed) to 8.98% (dominant), and bolewood decreased from 57.25% (suppressed) to 53.27% (dominant). Percentage of cones, needles, and roots increased slightly and percentage of dead branches decreased slightly with increasing tree size, but trends were not consistent.

The decrease in relative proportions of bolewood and bole bark and the increase in canopy and root components with increasing tree size have been recorded for a variety of species and site conditions: Norway spruce (Koršun 1940); Scots pine (Ovington and Madgwick 1959a); fir (Kuroiwa 1960a); balsam fir (Baskerville 1965b). A greater percentage increase in branchwood than foliage with increasing tree size noted by Burger (1940) for European beech was also noted for jack pine.

2. Stand

Distribution of biomass among all components of the stand is presented in Table 36. In terms of oven-dry weight, the above-ground standing crop is 63,836 kg/ha, the below-ground standing crop is 27,346 kg/ha, with the summation, the total standing crop, equal to 91,182 kg/hectare (1967). In comparison, the total organic matter for 20 coniferous stands (Rodin and Bazilevich 1967) representing a variety of sites and ages, range between 50,000 and 350,000 kg/hectare. Lower estimates are generally for xeric and hydric communities, with higher estimates for plantations.

Table 35. Percentage of total weight by component and tree size.[a]

Crown Class	Needles	Live Branches	Dead Branches	Cones	Bole (wob)	Bole Bark	Roots
	Mean % of Total Tree Weight[a]						
Suppressed (N=3)	4.73	6.68	3.28	0.48	57.25	11.96	15.56
Intermediate (N=6)	6.97	7.81	2.39	0.46	55.02	10.73	16.60
Codominant (N=7)	6.27	8.86	2.66	1.10	55.54	9.63	15.79
Dominant (N=4)	6.73	10.68	3.04	0.74	53.29	8.98	16.52
Total (N=20)	6.35	8.58	2.80	0.74	55.19	10.18	16.14

[a]Weight based on harvested samples.

Table 36. Distribution of biomass among stand components - 1967.

Component	Oven-Dry Weight (Kg/Ha)
Understory (N=30)	
Woody	771 ± 64
Non-woody	322 ± 27
Moss-lichen	2482 ± 226
Root-rhizome[a]	16074 ± 476
Arboreal[b]	
Needles	4840 (6.77% of total tree)
Live branch	6492 (9.07%)
Dead branch	1854 (2.59%)
Cones	596 (0.83%)
Bole (wob)	39664 (55.45%)
Bole bark	6815 (9.53%)
Roots	11272 (15.76%)
Total tree	71533 (100%)
Stand	
Total above-ground	63836
Total below-ground	27346
Summation	91182

[a]Estimate revised in text.

[b]Estimate based on summation of trees.

Among the various estimates of biomass, the contribution of mosses-ground lichen and small root-rhizome fractions to total biomass is particularly surprising. Cladonia lichen, often associated with poor site jack pine, represents less than 10% of the mosses-ground lichen component weight; thus, mosses contribute at least 2200 kg/ha to standing crop. Little mention is made in the literature of the importance of moss to xeric site biomass. The contribution of mosses to the stand biomass in hydric forests, however, may reach 5000 to 10,000 kg/ha and even 10,000 to 15,000 kg/ha in wooded moss bogs (Rodin and Bazilevich 1967). Information is also available concerning the standing crop of arboreal, epiphytic lichen. According to Scotter (1962) the air-dry weight of lichen on trees in the Black Lake district of northern Saskatchewan averages 1212 kg/ha in black spruce (<u>Picea</u> <u>mariana</u> (Mill.) B.S.P.) stands. No effort was made to separate arboreal lichen from bole bark in this study.

The root-rhizome fraction represents biomass of small roots ($<$ 0.5 inches in diameter) and rhizomes within the upper 10 cm of the soil profile. The estimate of 16,074 kg/ha, second only to bolewood in weight must be modified because of several limitations in the root-core sampling technique. (1) Despite the combination of washing and flotation used to separate organic soil fractions from inorganic fractions, mineral soil particles do remain. The mean ash content for 10 root samples muffled at 550 C was 12.98 $\pm$ 1.98% of oven-dry weight. Assuming 5% to be a normal ash content (Westlake 1963; Newbould 1967), the difference, 8%, is an indication of the amount of mineral soil retained in the sample after washing and flotation. (2) Significant amounts of organic matter other than roots were present in the core samples. Organic detritus such as litter fragments, small woody and charcoal fragments, dead arthropods, and dead root material cannot be separated from live roots by washing or flotation; non-root material averaged 25.79 ± 3.66% (N=10) of the oven-dry sample weight. Application of corrections for mineral particles and non-root materials reduces the root-rhizome estimate from 16,074 kg/ha to 11,125 kg/hectare. Despite the reduction, the biomass of feeder roots and rhizomes for all vegetation within the upper soil horizons of this rather xeric site is comparable to the biomass of the large structural roots of the trees.

The revised total below-ground biomass is 22,397 kg/ha, the total below-ground/total above-ground ratio is 1/2.85, and the total stand biomass estimate is 86,234 kg/hectare.

A twoway analysis of variance was applied to all understory fractions to test for significant differences in sample weights among transects, as well as among the three 0.1 acre study plots from which understory samples were taken. No significant differences ($P < .01$) were found, indicating the uniformity in study plots and the reduction in variance with transect plots. Transect weights for the most variable understory component, non-woody material, did differ significantly at the 95% probability level.

	transects (df=9,18)	0.1 acre plots (df=2,18)
non-woody	F = 2.7419 (*)	F = 2.1600 (NS)
woody	F = 1.0585 (NS)	F = 0.9880 (NS)
mosses-lichen	F = 1.7517 (NS)	F = 1.0408 (NS)

roots-rhizomes F = 0.8250 (NS) F = 0.1402 (NS)

total understory F = 1.7236 (NS) F = 0.4897 (NS)

A low variance among root core samples (coefficient of variation = 16.24%) reflects the uniform nature of the fine (absorptive) root mass within the upper soil horizons.

3. Litter Fall

To supplement the biomass data, litter fall samples were collected during the year prior to destructive sampling. Small litter fall (needles, twigs, strobili, bark) from the arboreal layer was collected in eight traps per 0.1 acre plot; traps were emptied every 3-4 weeks from July 1968 to July 1969.

The mean stand estimate of total arboreal litter production during this period, 1192.09 ± 98.26 kg/ha, is a mean of the estimates from the 0.1 acre plots:

plot A = 956.48 ± 88.55 kg/ha (N = 8)

plot B = 1267.24 ± 88.78 kg/ha (N = 8)

plot C = 1352.53 ± 72.90 kg/ha (N = 8)

The lower estimate for plot A reflects a lower tree density to the east and north of the plot. Needle fall during this period was 989.61 ± 79.84 kg/ha, or 83.0% of the total arboreal litter production. Again the stand estimate is a mean of the 0.1 acre plots:

plot A = 802.48 ± 35.00 kg/ha (N = 8)

plot B = 1033.98 ± 44.86 kg/ha (N = 8)

plot C = 1132.37 ± 59.62 kg/ha (N = 8)

Needle fall during the July 1968 to July 1969 period was 20.4% of the standing needle crop (1967). Total small litter fall was 8.7% of the total above-ground standing crop.

Inflorescences and fruits may account for a significant proportion of annual litter production. In a Minnesota study, aspen catkins equalled 25.8% of the oven-dry weight of leaf litter collected during 1959 and in a white pine stand, male cones equalled 6.3% of needle litter weight (Ovington 1963). For flowering dogwood (Cornus florida L.) trees growing in the open, fruiting structures accounted for 38% of the annual litter weight (Thomas 1967). For the Lake George jack pine stand, male cones constituted only 1.8% (21.46 kg/ha) of the total oven-dry litter production and equalled 2.2% of needle litter weight. For July and August collections, however, male cones did average 6% of the total litter, with a maximum of 30% for individual traps.

Other fractions of the litter production include small twigs, 5.1% or 60.79 ka/ha, and a miscellaneous category, 10.1% or 120.40 kg/ha, consisting mainly of bark chips and insect frass. The contribution of insect frass, although not specifically separated and weighed, was certainly greater than that of the inflorescences.

As expected, leaf litter production for the Lake George jack pine is lower than most estimates for coniferous stands in a temperate climate (Table 37). For cool temperate forests, Bray and Gorham (1964) cite a total annual litter production of 3500 kg/ha and annual leaf litter production of 2500 kg/ha (Table 38). The low litter production for the Lake George jack pine site is a function of the single-layered structure and the relatively thin canopy structure supported on the xeric site.

The seasonal litter fall pattern exhibits a bimodal distribution with a primary peak in the fall and a secondary peak in the spring

Table 37. Annual leaf litter production in coniferous stands.

Species	Stand Data	Leaf Litter Fall (Kg/Ha)	Source
Jack pine	51 yr-natural	990$\pm$80	Crow (present study)
Jack pine	30-55 yr-natural	2300-2600	Alway and Zon (1930)
Jack pine	30-250 yr-natural	2200-2500	Kittredge (1948)
White pine	65 yr-plantation	3100	Chandler (1944)
White pine	65 yr-natural	3100	Alway and Zon (1930)
White pine	natural	2300-3400	Lutz and Chandler (1946)
White pine	30-250 yr-natural	2200-2500	Morgan and Lunt (1931)
White pine	25 yr-plantation	5140	Rodin and Bazilevich (1967)
Red pine	25 yr-plantation	3800	Chandler (1944)
Red pine	natural	1970	Alway and Zon (1930)
Scots pine	80-107 yr-natural	3600	Rodin and Bazilevich (1967)
Scots pine	14 yr-natural	2500	"
Scots pine	32 yr-natural	2360	"
Scots pine	45 yr-natural	1910	"
Scots pine	71 yr-natural	2000	"
Scots pine	94 yr-natural	1300	"

Table 38. Annual litter production in major climatic zones of the world (Bray and Gorham 1964).

Climatic Zone	Litter Production (Kg/Ha)	
	Total	Leaf
Arctic-alpine (67 deg N Lat)	1000	700
Cool-temperate (37-62 deg N Lat)	3500	2500
Warm-temperate (30-40 deg N Lat)	5500	3600
Equatorial ($\pm$10 deg of equator)	10900	6800

(Fig. 2). Collections during October and November account for 46.7% of the annual total, with an additional 19.3% collected during June and July. Collections were minimal during the early spring months of March and April.

Because annual litter production varies greatly, measurements for a single year can serve only as an indicator. Longevity of Gymnosperm needles is a function of both internal and external mechanisms (storms, insect attack, drought, cold temperatures), thus annual variation in litter production tends to be greater for coniferous species than for deciduous species (Bray and Gorham 1964). Maximum/minimum annual litter production ratios for coniferous stands cited by Bray and Gorham (1964) range from 5.2 to 1.3, compared to a range of 1.8 to 1.1 for deciduous Angiosperms. For red pine and jack pine stands in northern Minnesota, Alway and Zon (1930) found litter production to vary as much as 25% from year to year. During 21 years of sampling, Lunt (1951) recorded a max/min ratio of 3.4 in a stand of red pine. In the classic work by Ebermayer (1876), the max/min ratios for litter production in pine stands were generally 2 or 3.

4. Macro-litter

Concurrent with small litter collections, macro-litter was collected from the center 0.05 acre of each 0.1 acre plot. The large items of litter, consisting mainly of branches, averaged 147.65 ± 61.41 kg/ha (N=3). The variation of macro-litter in time and space is reflected by the large standard error of mean. Combined with the small litter estimation, the total litter production from July 1968 to July 1969 for the study site equalled 1340 kg/hectare.

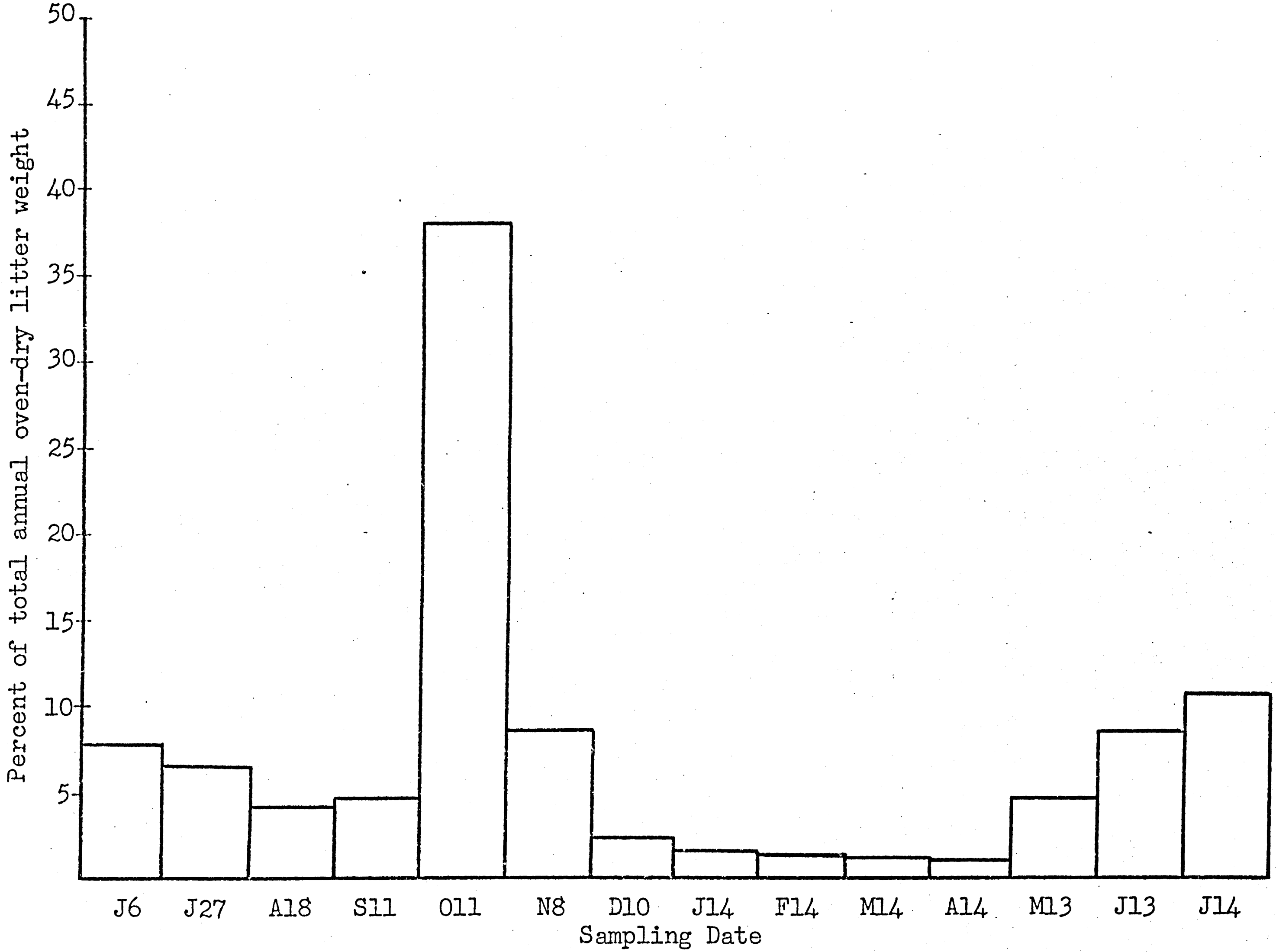

Fig. 2. Distribution of total litter fall during sample period (July 7, 1968 to July 14, 1969). All sample weights prorated to a 30 day sampling period to provide a uniform time scale.

VI. SUMMARY AND CONCLUSIONS

The major objective of this study was the evaluation of various techniques for biomass determination in a jack pine stand (age = 51.3 yrs; SI = 40.6 ft). A secondary objective was the determination of biomass distribution among all stand components.

It is evident from the evaluation of various regression curve forms and independent variables for the estimation of biomass that no single curve form or independent variable consistently produces the most reliable fit for all components. The best general form proved to be curve (3)

$$Y = AX^B$$

with DBH as the independent variable; the linear transformation of curve (3)

$$\log Y = \log A + B \log X$$

is the most common form cited in the literature. The strong exponential trend between biomass and a measurable parameter cited for many species is not evident for the even-aged jack pine. For most components, the more convenient linear regression could be used with only a slight reduction in reliability. The independent variable DBH proved superior to bole diameter-tree base, bole diameter-base of crown, and canopy volume. Use of canopy height and total tree height as independent variables resulted in relatively low correlations. Because π is a constant, the independent variable DBH^2 should be substituted for cross-sectional area at DBH, regardless of the curve form. When using curve (3), the same fit is obtained regardless if the independent variable is DBH or DBH^2, and of course, cross-sectional area at DBH. Substitution of D^2H for DBH generally did not improve the accuracy of the regression estimate.

Little advantage was found in using multiple regressions in place of simple allometric functions. For estimates of total tree weight, inclusion of total height as a variable did not make a significant reduction in the mean square residuals when fitted after DBH. The form

$$\log_e Y = B_0 + B_1 \log_e(\text{DBH}) + B_2 \log_e(\text{total tree height}),$$

often cited in the literature, was not significantly different from

$$\log_e Y = B_0 + B_1 \log_e(\text{DBH})$$

for the Lake George jack pine.

The regression equation for needle weight estimation in this study

$$\log_{10} W = 2.8471 \log_{10}\text{DBH} - 1.475$$

is extremely close to that cited for Minnesota jack pine by Kittredge (1944,1948)

$$\log_{10} W = 2.87 \log_{10}\text{DBH} - 1.58 \qquad (\text{age} = 37 \text{ yrs; SI} = 45 \text{ ft}).$$

More information is needed on the validity of applying a common regression to the same species on different sites. However, the potentials are promising for simply structured stands such as plantations or pure stands of even-aged individuals.

Stand estimates of oven-dry weight for each component were derived from a summation of estimates for all 180 trees within the study plots using that curve form and independent variable giving the most reliable estimate. The strongest correlations were obtained with the following equations:

needles	$Y = AX^B$	$X = D^2H$
live branches	$Y = AX^B$	X = DBH; DBH^2; or cross-sectional area at DBH
cones	$Y = A + BX$	X = cross-sectional area at base of tree
dead branches	$Y = Ae^{BX}$	X = DBH
bole (wob)	$Y = AX^B$	X = DBH; DBH^2; or cross-sectional area at DBH
bole bark	$Y = AX^B$	$X = D^2H$
roots	$Y = AX^B$	X = DBH; DBH^2; or cross-sectional area at DBH

In the evaluation of stand estimates based on a single tree of mean dimension, successive improvements are noted with estimates based on a tree of mean total height, mean total height X mean DBH, mean DBH, and mean BA. Compared to an every-tree summation, total stand biomass is underestimated by 23.4% and individual components by as much as 32.5% when based on a tree of mean total height. When based on the tree of mean BA, total tree biomass is underestimated by only 2.1%, with a maximum deviation of -7.3% for dead branches. Estimates based on the tree of mean bole (wob) volume generally overestimate the biomass. The total tree biomass is overestimated by 2.8%, with a maximum deviation of +5.0% for cones. Estimates based on individuals at ± one standard deviation from a stand mean are superior to "mean tree" estimates. When stand estimates are based on diameters at ± one standard deviation from mean stand DBH, deviations for all components are 1% and less.

It is evident that estimates based on a "mean tree" may be valid for certain community structures and study requirements. Deviations of "mean tree" estimates from the every-tree summation for the even-aged, uniform jack pine stand are substantially less than those reported for the more complex, all-aged stands.

Distribution of biomass among stand components was as follows:

Understory (N = 30)	
woody	771 ± 64 kg/ha (oven-dry wt)
non-woody	322 ± 27 kg/ha
moss-lichen	2482 ± 226 kg/ha
root-rhizome	16074 ± 476 kg/ha
Arboreal (based on summation of trees)	
needles	4840 kg/ha (6.77% of total tree)
live branch	6492 kg/ha (9.07%)
dead branch	1854 kg/ha (2.59%)
cones	596 kg/ha (0.83%)
bole (wob)	39664 kg/ha (55.45%)
bole bark	6815 kg/ha (9.53%)
roots	11272 kg/ha (15.76%)
total tree	71533 kg/ha
Stand	
total above-ground	63836 kg/ha
total below-ground	27346 kg/ha
summation	91182 kg/ha

Particularly surprising are the contributions of moss-ground lichen and small root-rhizome fractions to the total standing crop on this rather xeric site. The root-rhizome fraction represents biomass of roots less than 0.5 inches in diameter and rhizomes extracted from the upper 10 cm of the soil horizon with a core sampler. Application of corrections for mineral particles and non-root materials within the final core sample reduces this estimate from 16,074 to 11,125 kg/ha, still a substantial figure.

The mean stand estimate of total arboreal litter production during the year prior to destructive sampling was 1192.09 $\pm$ 98.26 kg/hectare. Needle fall during this period was 989.61 $\pm$ 79.84 kg/ha, or 83.0% of the total arboreal litter production. Other fractions of the litter production include small twigs, 5.1% or 60.79 kg/ha; inflorescences and fruits, 1.8% or 21.46 kg/ha; and a miscellaneous category, 10.1% or 120.40 kg/ha, consisting mainly of bark chips and insect frass. Collections during October and November account for 46.7% of the annual total. The annual needle fall was 20.4% of the standing needle crop (1967).

Macro-litter fall, mainly large branches, averaged 147.65 $\pm$ 61.41 kg/ha during the same collection period.

VII. APPENDIX

Table 1. Flora List

Genus - Species	Presence		
	Plot A	Plot B	Plot C
Trees			
Picea glauca (Moench) Voss	X		
Pinus banksiana Lamb.	X	X	X
Pinus resinosa Ait.	X		
Quercus macrocarpa Michx.	X		
Quercus rubra L.	X	X	X
Shrubs			
Amelanchier humilis Wieg.	X	X	X
Corylus americana Walt.		X	
Corylus cornuta Marsh.		X	X
Prunus pumila L.	X	X	X
Rosa blanda Ait.		X	X
Salix humilis Marsh.	X		X
Symphoricarpos albus L.		X	
Half-Shrubs			
Arctostaphylos uva-ursi (L.) Spreng.	X	X	X
Chimaphila umbellata (L.) Bart.		X	
Gaultheria procumbens L.	X	X	X
Vaccinium angustifolium Ait.	X	X	X
Forbs			
Achillea lanulosa Nutt.		X	X
Anenome quinquefolia L.	X	X	X
Antennaria fallax Greene	X	X	X
Antennaria neodioica Greene	X	X	X
Apocynum androsaemifolium L.	X	X	X
Aster laevis L.	X	X	X
Aster macrophyllus L.		X	
Campanula rotundifolia L.	X	X	X
Convolvulus spithamaeus L.	X	X	X
Erigeron strigosus Muhl.		X	X
Fragaria vesca Porter	X	X	
Fragaria virginiana Duchesne	X		X
Galium boreale L.	X	X	X
Lathyrus ochroleucus Hook.	X	X	X
Liatris aspera Michx.	X		
Lilium philadelphicum L.		X	X
Linnaea borealis L.	X	X	X
Lithospermum canescens (Michx.) Lehm.	X	X	X
Maianthemum canadense Desf.	X	X	

Table 1, continued

Forbs, continued			
Melampyrum lineare Desr.	X	X	X
Pedicularis canadensis L.	X		
Petasites sagittatus (Pursh) Gray	X		
Prenanthes alba L.			X
Pyrola rotundifolia L.	X	X	X
Rhus radicans L.			X
Senecio pauperculus Michx.			X
Solidago hispida Muhl.		X	X
Solidago nemoralis Ait.	X	X	X
Taraxacum officinale Weber.		X	
Vicia caroliniana Walt.		X	
Viola adunca Sm.	X	X	X
Zizia aptera (Gray) Fern.	X		
Ferns			
Pteridium aquilinum (L.) Kuhn			X
Grasses			
Andropogon sp.	X		
Bromus tectorum L.	X	X	X
Danthonia spicata (L.) Beauv.	X	X	X
Oryzopsis pungens (Torr.) Hitchc.	X	X	X
Panicum sp.			X
Sporobolus sp.		X	
Mosses and Lichens			
Cladonia rangiferina (L.) Web.	X	X	X
Pleurozium schreberi (Brid.) Mitt.	X	X	X
Polytrichum juniperinum Hedw.	X	X	X

Table 2. Soil Description

Soil Type	Horizon	Depth (inches)	Color, moist	Structure
		Plot A		
	O1	1-0		
	A1	0-2	10YR 2/2	single grained; many roots
Menahga loamy sand	A2	2-4	10YR 4/3	single grained; loose
	B2	4-16	10YR 5/4	single grained; gradual boundary
	B3	16-21	10YR 5/6	"
	C	21+	10YR 5/4	"
		Plot B		
	O1	1-0		
	A2	0-4	10YR 3/4	single grained
Menahga loamy sand	B1	4-10	10YR 4/4	single grained
	B2	10-17	10YR 5/4	single grained
	B3	17-27	10YR 5/6	occasional gravel
	C	27+	10YR 5/4	"
		Plot C		
	O1	1-0		
	A1	0-1	10YR 3/2	single grained
Menahga loamy sand	A2	1-4	10YR 4/3	single grained
	B2	4-14	10YR 5/4	occasional gravel
	B3	14-24	10YR 5/6	"
	C	24+	10YR 5/4	"

Table 3. Soil Analysis

Horizon	pH	P(ppm)	K(ppm)	Texture (%) (< 2mm) Sand	Silt	Clay
			Plot A			
01						
A1	6.7	13	80	84.5	7.9	7.6(loamy sand)
A2	6.6	15	40	86.4	8.6	5.0(loamy sand)
B2	6.4	25	45	84.6	11.8	6.6(loamy sand)
B3	6.5	80	30	91.2	5.2	3.6(sand)
C	6.5	41	20	95.9	< 1	3.6(sand)
			Plot B			
01						
A2	6.1	15	75	86.4	9.6	4.0(loamy sand)
B1	6.0	26	45	82.2	8.2	9.6(loamy sand)
B2	6.2	58	25	90.0	1.4	8.6(loamy sand)
B3	6.4	75	20	92.0	< 1	7.6(sand)
C	6.6	10	10	97.3	< 1	2.6(sand)
			Plot C			
01						
A1	6.0	6	100	76.6	11.8	8.6(sandy loam)
A2	6.2	21	65	83.3	13.1	3.6(loamy sand)
B2	6.3	40	40	83.3	5.1	11.6(loamy sand)
B3	6.4	43	20	92.9	< 1	6.6(sand)
C	6.9	5	10	95.0	< 1	4.1(sand)

VIII. ACKNOWLEDGMENTS

The author wishes to express his appreciation to his major advisor, Dr. Henry L. Hansen, and to the Director of the School of Forestry, Dr. Frank H. Kaufert, for making this research possible. Appreciation is extended to Dr. Egolfs V. Bakuzis for his generous assistance throughout the study; to Dr. Douglas Gerrard for assistance with statistical procedures; to Dr. Alan J. Brook and Dr. Edward J. Cushing for their constructive comments on the manuscript; to Dr. William H. Marshall and Dr. Alvin R. Hallgren for allowing use of laboratory facilities at the University of Minnesota Forestry and Biological Station at Lake Itasca.

I sincerely thank the numerous people who helped at various stages of field sampling. A special acknowledgment is due to William A. Patterson for the hours of tedious field work which he endured.

Appreciation is also due to the Northwest Paper Company and their area representative, Mr. Donald E. Pierce, for allowing location of study plots and subsequent destructive sampling on their Lake George Unit.

IX. LITERATURE CITED

Adams, W.R. 1928. Studies in tolerance of New England forest trees. VIII. Effect of spacing in a jack pine plantation. Vermont Agr. Expt. Sta. Bull. 282. 55 p.

Alway, F.J. and R. Zon. 1930. Quantity and nutrient contents of pine leaf litter. J. For. 28: 715-727.

Andersson, F. 1970. Ecological studies in a scanian woodland and meadow area, southern Sweden. II. Plant biomass, primary production and turnover of organic matter. Bot. Notiser 123: 8-51.

Ando, T.K., K. Hatuja, and K. Doi. 1959. Estimation of the amount of leaves, twigs, and branches of Sugi (Cryptomeria japonica D. Don) by sampling method. J. Jap. For. Soc. 41: 117-124. Abstract in For. Abst. 23: 997.

Ando, T.K., K. Sakaguchi, T. Narita, and S. Satoo. 1962. Growth analysis on the natural stands of Japanese red pine (Pinus densiflora Sieb. et Zucc.). I. Effects of improvement cutting and relative growth [in Japanese, English summary]. Bull. Gov. For. Expt. Sta. (Tokyo) 44: 1-30.

Arneman, H.F. 1963. Soils of Minnesota. Univ. Minn. Agr. Ext. Service Bull. 287. 8 p.

Assmann, E. 1961. Waldertragskunde. Organische Production, Structure, Zuwachs und Ertrag von Waldbestanden. BLV Verlagsgesellschaft Munchen, Bonn Wien. 490 p.

Attiwill, P.M. 1962. Estimating branch dry weight and leaf area from measurements of branch girth in Eucalyptus. For. Sci. 8: 132-141.

Attiwill, P.M. 1966. A method for estimating crown weight in Eucalpytus and some other implications of relationships between crown weight and stem diameter. Ecology 47: 795-804.

Baker, D.G., D.A. Haines, and J.H. Strub. 1967. Climate of Minnesota. Part V. Precipitation facts, normals, and extremes. Univ. Minn. Agr. Expt. Sta. Tech. Bull. 254. 43 p.

Baker, D.G. and J.H. Strub. 1963. Climate of Minnesota. Part II. The agricultural and minimum-temperature-free seasons. Univ. Minn. Agr. Expt. Sta. Tech. Bull. 245. 31 p.

Baker, D.G. and J.H. Strub. 1965. Climate of Minnesota. Part III. Temperature and its application. Univ. Minn. Agr. Expt. Sta. Tech. Bull. 248. 63 p.

Baskerville, G.L. 1965a. Dry-matter production in immature balsam fir stands. For. Sci. Monograph 9. 42 p.

Baskerville, G.L. 1965b. Estimation of dry weight of tree components and total standing crop in conifer stands. Ecology 46: 867-869.

Bella, I.E. 1968. Estimating aerial component weights of young aspen trees. Canada Dept. For. and Rural Develop., For. Res. Lab., Winnipeg. Information Report MS-X-12. 36 p.

Bray, J.R. 1960. The chlorophyll content of some native and managed plant communities in central Minnesota. Can. J. Bot. 38: 313-333.

Bray, J.R. 1963. Root production and the estimation of net productivity. Can. J. Bot. 41: 65-72.

Bray, J.R. and L.A. Dudkiewicz. 1963. The composition, biomass and productivity of two Populus forests. Bull. Torrey Bot. Club 90: 298-308.

Bray, J.R. and E. Gorham. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2: 101-157.

Bray, J.R., D.B. Lawrence, and L.C. Pearson. 1959. Primary production in some Minnesota terrestrial communities for 1957. Oikos 10: 38-49.

Brown, J.K. 1963. Crown weight in red pine plantations. U.S. For. Serv. Lakes States Expt. Sta. Research Note LS-19. 4 p.

Brown, J.K. 1965. Estimating crown fuel weights of red pine and jack pine. U.S. For. Serv. Lake States Expt. Sta. Research Paper LS-20. 12 p.

Brown, R.M. and S.R. Gevorkiantz. 1934. Volume, yield, and stand tables for tree species in the Lake States. Minn. Agr. Expt. Sta. Tech. Bull. 39. 208 p.

Burger, H. 1937. Holz, Blattmenge und Zuwachs. III. Nadelmenge und Zuwachs bei Föhren und Fichten verschiedener Herkunft. Mitt. schweiz. Anst. forstl. Versuchsw. 20: 112-137.

Burger, H. 1940. Holz, Blattmenge und Zuwach. IV. Ein 80 jähriger Buchenbestand. Mitt. schweiz. Anst. forstl. Versuchsw. 21: 307-348. Abstract in For. Abst. 3: 175-176.

Burger, H. 1941. Holz, Blattmenge und Zuwachs. V. Fichten und Föhren verschiedener Herkunft auf verschiedenen Kulturorten. Mitt. schweiz. Ant. forstl. Versuchsw. 22: 10-62. Abstract in For. Abst. 4: 135-136.

Burger, H. 1950. Holz, Blattmenge und Zuwachs. X. Die Buche. Mitt. schweiz. Anst. forstl. Versuchsw. 26: 419-468.

Burger, H. 1951. Holz, Blattmenge und Zuwach. XI. Die Tanne. Mitt. schweiz. Anst. forstl. Versuchsw. 27: 247-286.

Burger, H. 1952. Holz, Blattmenge und Zuwach. XII. Fichten im Plenterwald. Mitt. schweiz. Anst. forstl. Versuchsw. 28: 109-156.

Cable, D.R. 1958. Estimating surface area of ponderosa pine foliage in central Arizona. For. Sci. 4: 45-49.

Chandler, R.F. 1944. Amount and mineral nutrient content of freshly fallen needle litter of some north-eastern conifers. Proc. Soil Sci. Soc. Amer. 8: 409-411.

Chapman, H.H. and W.H. Meyer. 1949. Forest mensuration. McGraw-Hill Book Co., New York. 522 p.

Chase, C.D. 1964. Forest type area by counties, Minnesota, 1962. U.S. For. Serv. Lakes States Expt. Sta. Research Note LS-55. 2 p.

Christidis, B.G. 1931. The importance of the shape of plots in field experimentation. J. Agr. Sci. 21: 14-37.

Clapham, A.R. 1932. The form of the observational unit in quantitative ecology. J. Ecol. 20: 192-197.

Cole, D.W., S.P. Gessel, and S.F. Dice. 1967. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-fir ecosystem, p. 198-232. In Symposium on primary productivity and mineral cycling in natural ecosystems. Univ. Maine Press, Orono.

Dyer, R.F. 1967. Fresh and dry weight, nutrient elements and pulping characteristics of northern white cedar (*Thuja occidentalis*). Maine Agr. Expt. Sta. Tech. Bull. 27. 39 p.

Dyer, R.F., A.J. Chase, and H.E. Young. 1968. Pulp from present non-commercial woody perennials. Pulp and Paper Mag. of Canada, Tech. Paper T1: 57-62.

Ebermayer, E. 1876. Die gesammte Lehre der Waldstreu mit Rücksicht auf die chemische Statik des Waldbaues. Julius Springer, Berlin. 116 p.

Erteld, W. and E. Hengst. 1966. Waldertragslehre. Neumann Verlag, Radebeul. 322 p.

Ezekiel, M. and K.A. Fox. 1959. Methods of correlation and regression analysis. 3 ed. John Wiley and Sons, Inc., New York. 548 p.

Forrest, W.G. 1968. The estimation of oven-dry weight. Australian For. Res. 3: 41-46.

Freese, F. 1962. Elementary forest sampling. U.S. Dept. Agr. Handbook No. 232. 91 p.

Freese, F. 1964. Linear regression methods for forest research. U.S. For. Serv. Forest Products Lab. Research Paper 17. 138 p.

Furnival, G.M. 1961. An index for comparing equations used in constructing volume tables. For. Sci. 7: 337-341.

Golley, F., H.T. Odum, and R.F. Wilson. 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. Ecology 43: 9-19.

Hall, G.S. 1965. Wood increment and crown distribution relationships in red pine. For. Sci. 11: 438-448.

Hansen, H.L. 1946. An analysis of jack pine sites in Minnesota with special reference to site index, plant indicators, and certain soil features. Ph.D. Thesis. Univ. Minnesota. 115 p.

Hansen, T.S. 1937. Ecological changes due to thinning jack pine. Minn. Agr. Expt. Sta. Tech. Bull. 124. 77 p.

Heiberg, S.O., L. Leyton, and H. Loewenstein. 1959. Influence of potassium fertilizer level on red pine planted at various spacings on a potassium deficient site. For. Sci. 5: 142-153.

Hozumi, K. 1963. Allometry in higher plants -- with special reference to the relations concerned with DBH [in Japanese]. Seichô (J. of Growth) 2: 1-18.

Hozumi, K., K. Yoda, S. Kodawa, and T. Kira. 1969. Production ecology of tropical rain forests in southwestern Cambodia. I. Plant biomass. Nature and Life in Southeast Asia 6: 1-51.

Hutnik, R.T. 1964. Accumulation and production of dry matter in red pine plantations of various spacings. Ph.D. Thesis. Duke Univ. 207 p.

Il'inskij, V.V. 1968. Biomass of pine in stands of different site classes [in Russian]. Lesnoe Khoziaistvo 3:34.

Iwaki, H. 1958. The influence of density on the dry matter production of Fagropyrum esculentum. Jap. J. Bot. 16: 210-226.

Jahnke, L.S. and D.B. Lawrence. 1965. Influence of phytosynthetic crown structure on potential productivity of vegetation based primarily on mathematical models. Ecology 46: 319-326.

Kimura, M. 1963. Dynamics of vegetation in relation to soil development in northern Yatsugadake Mountains. Jap. J. Bot. 18: 255-287.

Kira, T., H. Ogawa, K. Yoda, and K. Ogino. 1964. Primary production by a tropical rain forest of southern Thailand. Bot. Mag. Tokyo 77: 428-429.

Kittredge, J. 1944. Estimation of the amount of foliage of trees and stands. J. For. 42: 905-912.

Kittredge, J. 1948. Forest influences. McGraw-Hill Book Co., New York. 394 p.

Koršun, F. 1940. The bark and limb percent of Norway spruce [in Czech.]. Lesnicka' Prace' 19: 23-31. Abstract in For. Abst. 3: 85.

Küchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geographical Society. Special Pub. No. 36. 116 p. + map.

Kurmis, V. and H.L. Hansen. 1969a. Reproduction characteristics of upland forest communities in Itasca State Park, Minnesota. Minn. For. Res. Notes No. 209. 4 p.

Kurmis, V. and H.L. Hansen. 1969b. Occurrence and distribution of pine reproduction in Itasca State Park, Minnesota. Minn. For. Res. Notes No. 210. 4 p.

Kuroiwa, S. 1959. Ecological and physiological studies on the vegetation of Mt. Shimagare. III. Intraspecific competition and structural development of the <u>Abies</u> forest. Bot. Mag. Tokyo 72: 413-421.

Kuroiwa, S. 1960a. Ecological and physiological studies on the vegetation of Mt. Shimagare. IV. Some physiological functions concerning matter production in young <u>Abies</u> trees. Bot. Mag. Tokyo 73: 133-141.

Kuroiwa, S. 1960b. Ecological and physiological studies on the vegetation of Mt. Shimagare. V. Intraspecific competition and productivity differences among tree classes in the *Abies* stand. Bot. Mag. Tokyo 73: 165-174.

Loomis, R.M., R.E. Phares, and J.S. Crosby. 1966. Estimating foliage and branchwood quantities in shortleaf pine. For. Sci. 12: 30-39.

Lunt, H.A. 1935. Effect of weathering upon dry matter and composition of hardwood leaves. J. For. 33: 607-609.

Lunt, H.A. 1951. Liming and twenty years of litter raking and burning under red (and white) pine. Proc. Soil Sci. Soc. Amer. 15: 381-390.

Lutz, H.J. and R.F. Chandler. 1946. Forest soils. John Wiley and Sons, Inc., New York. 514 p.

Madgwick, H.A.I. 1967. Some factors affecting the vertical distribution of foliage in pine canopies, p. 233-245. *In* Symposium on primary productivity and mineral cycling in natural ecosystems. Univ. Main Press, Orono.

Madgwick, H.A.I. 1968. Seasonal changes in biomass and annual production of an old-field *Pinus virginiana* stand. Ecology 49: 149-152.

Maruyama, I. and T. Satoo. 1953. Estimation of the amount of foliage of trees and stands. (Report 1) -- on the Akamatu of Iwate District [in Japanese, English summary]. Bull. Govt. Forest Expt. Sta. (Tokyo) 65: 1-10.

Möller, C.M. 1945. Untersuchungen über Laubmenge, Stoffverlust und Stoffproduktion des Waldes. Forst. Forsogsv. Danmark 17: 1-287.

Möller, C.M. 1947. The effect of thinning, age and site on foliage, increment and loss of dry matter. J. For. 45: 393-404.

Möller, C.M. 1954. The influence of thinning on volume increment, p. 5-44. In Thinning problems and practices in Denmark. World For. Bull. 1, Coll. of For., Syracuse.

Möller, C.M., D. Müller, and J. Nielsen. 1954a. Graphic presentation of dry matter production of European beech. Forst. Forsogsv. Danmark 21: 327-335.

Möller, C.M., D. Müller, and J. Nielsen. 1954b. Respiration in stem and branches of beech. Forst. Forsogsv. Danmark 21: 273-301.

Morgan, M.F. and H.A. Lunt. 1931. The role of organic matter in the classification of forest soil. J. Am. Soc. Agron. 23: 1059-1060.

Newbould, P.J. 1967. Methods for estimating the primary production of forests. IBP Handbook No. 2. Blackwell Scientific Publications, Oxford and Edinburgh. 62 p.

Ogawa, H., K. Yoda, and T. Kira. 1961. A preliminary survey on the vegetation of Thailand. Nature and Life in S.E. Asia 1: 21-157.

Ogawa, H., K. Yoda, and T. Kira. 1965. (Ogawa et al. 1965a). Comparative ecological studies on three main types of forest vegetation in Thailand. I. Structure and floristic composition. Nature and Life in S.E. Asia 4: 13-48.

Ogawa, H., K. Yoda, K. Ogino, and T. Kira. 1965. (Ogawa et al. 1965b). Comparative ecological studies on three main types of forest vegetation in Thailand. II. Plant biomass. Nature and Life in S.E. Asia 4: 49-80.

Ogino, K., S. Sabhasri, and T. Shidei. 1964. The estimation of the standing crop of the forest in northern Thailand. The S.E. Asian Studies 4: 89-97.

Olson, J.S. 1959. Exponential equations relating productivity, decay, and accumulation of forest litter. 9th Int. Bot. Congr. 2: 287.

Olson, J.S. 1964. Gross and net production of terrestrial vegetation, p. 99-118. In A. MacFadyen and P.J. Newbould (ed.) Jubilee Symposium British Ecological Society.

Ovington, J.D. 1956. The form, weights, and productivity of tree species grown in close stands. New Phytologist 55: 289-304.

Ovington, J.D. 1957. Dry-matter production by Pinus sylvestris L. Ann. Bot. N.S. 21: 287-314.

Ovington, J.D. 1961. Some aspects of energy flow in plantations of Pinus sylvestris L. Ann. Bot. N.S. 25: 12-20.

Ovington, J.D. 1963. Flower and seed production. A source of error in estimating woodland production, energy flow and mineral cycling. Oikos 14: 148-153.

Ovington, J.D., W.G. Forrest, and J.S. Armstrong. 1967. Tree biomass estimation, p. 4-31. In Symposium on primary productivity and mineral cycling in natural ecosystems. Univ. Main Press, Orono.

Ovington, J.D. and H.A.I. Madgwick. 1959a. Distribution of organic matter and plant nutrients in a plantation of Scots pine. For. Sci. 5: 344-354.

Ovington, J.D. and H.A.I. Madgwick. 1959b. The growth and composition of natural stands of birch. I. Dry-matter production. Plant and Soil 10: 271-288.

Ovington, J.D. and W.H. Pearsall. 1956. Production ecology. II. Estimates of average production of trees. Oikos 7: 202-205.

Pearson, L.C. 1965. Primary production in grazed and ungrazed desert communities of eastern Idaho. Ecology 46: 278-285.

Pearson, L.C. 1966. Primary productivity in a northern desert area. Oikos 15: 211-228.

Pearsall, W.H. and E. Gorham. 1956. Production ecology. I. Standing crops of natural vegetation. Oikos 7: 193-201.

Rennie, P.J. 1966. A forest sampling procedure for nutrient-uptake studies. Comm. For. Review 45: 119-127.

Rodin, L.E. and N.I. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation [transl. from Russian]. Oliver and Boyd, Edinburgh and London. 288 p.

Rothacker, J.S., F.E. Blow, and S.M. Potts. 1954. Estimating the quantity of tree foliage in oak stands in the Tennessee Valley. J. For. 52: 169-173.

Rutter, A.J. 1957. Studies in the growth of young plants of Pinus sylvestris. I. The annual cycle of assimilation and growth. Ann. Bot. N.S. 21: 399-425.

Satoo, T. 1962. Notes on Kittredge's method of estimation of amount of leaves of forest stand. J. Jap. For. Soc. 44: 267-272.

Satoo, T. 1966. Production and distribution of dry matter in forest ecosystems. Misc. Information, Tokyo Univ. For. 16: 1-15.

Satoo, T. 1967a. Efficiency and quantity of leaves of closed stands of Cryptomeria japonica as influenced by site quality, p. 395-404. In Inter. Union For. Research Organization 14th Congress, Vol. 2.

Satoo, T. 1967b. Primary production relations in woodlands of Pinus densiflora, p. 52-80. In Symposium on primary productivity and mineral cycling in natural ecosystems. Univ. Maine Press, Orono.

Satoo, T., R. Kunugi, and A. Kumekawa. 1956. Materials for the studies of growth in stands. 3. Amount of leaves and production of wood in an aspen (Populus davidiana) second growth in Hokkaida [in Japanese, English summary]. Bull. Tokyo Univ. For. 52: 33-51.

Satoo, T., K. Nakamura, and S. Senda. 1955. Materials for the studies of growth in stands. I. Young stands of Japanese red pine of various density [in Japanese, English summary]. Bull. Tokyo Univ. For. 48: 65-90.

Satoo, T., N. Negisi, and M. Senda. 1959. Materials for the studies of growth in stands. V. Amount of leaves and growth in plantations of Zelkowa serrata applied with crown thinning [in Japanese, English summary]. Bull. Tokyo Univ. For. 55: 101-123.

Satoo, T. and M. Senda. 1958. Materials for the studies of growth in stands. IV. Amount of leaves and production of wood in a young plantation of Chamaecyparis obtusa [in Japanese, English summary]. Bull. Tokyo Univ. For. 54: 71-100.

Scooter, G.W. 1962. Productivity of arboreal lichen and their possible importance to barrenground caribou (Rangifer arcticus). Arch. Soc. Zool. Brotan. Fennicae 16: 155-161.

Senda, M. and T. Satoo. 1956. Materials for the study of growth in stands. 2. White pine (Pinus strobus) stands of various densities in Hokkaido [in Japanese, English summary]. Bull. Tokyo Univ. For. 52: 15-31.

Senda, S., K. Nakamura, S. Takahara, and T. Satoo. 1952. Some aspects of growth in stands (a preliminary report). An analysis of pine stands of different spacing [in Japanese, English summary]. Bull. Tokyo Univ. For. 43: 49-57.

Shanks, R.E. and E.E.C. Clebsch. 1962. Computer program for the estimation of forest stand weight and mineral pool. Ecology 43: 339-341.

Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964. A quantitative analysis of plant form -- the pipe model theory. Jap. J. Ecol. 14: 97-105, 133-139.

Smith, D.M. 1962. The practice of silviculture. John Wiley and Sons, Inc., New York. 578 p.

Society of American Foresters. 1954. Forest cover types of North America. 4th ed. Washington, D.C. 67 p.

Stephens, G.R. 1969. Productivity of red pine. 1. Foliage distribution in tree crown and stand canopy. Agr. Meteorol. 6: 275-282.

Stiell, W.M. 1962. Crown structure in plantation red pine. Canada Dept. For. Tech. Note 122. 36 p.

Sukachev, V. and N. Dylis. 1964. Fundamentals of forest biogeocoenology [translated from Russian]. Oliver and Boyd, Edinburgh and London. 672 p.

Tadaki, Y. 1966. Some discussions on the leaf biomass of forest stands and trees. Bull. Gov. For. Expt. Sta. (Tokyo) 184: 135-161.

Tadaki, Y. and T. Shidei. 1960. Studies of productive structure of forests. 1. The seasonal variation of leaf amount and the dry matter production of deciduous sampling stand (Ulmus parviflora). J. Jap. For. Soc. 42: 427-434.

Thomas, W.A. 1967. Accumulation and cycling of calcium by flowering dogwood trees. Ph.D. Thesis. Univ. Minn. 152 p.

Verduin, J., E. Eloise Whitwer, and B.C. Cowell. 1959. Maximal photosynthetic rates in nature. Science 130: 268-269.

Wackerman, A.E., R. Zon, and F.G. Wilson. 1929. Yield of jack pine in the Lake States. Wisconsin Agr. Expt. Sta. Res. Bull. 90. 24 p.

Weetman, G.F. and R. Harland. 1964. Foliage and wood production in unthinned black spruce in Northern Quebec. For. Sci. 10: 80-88.

Westlake, D.F. 1963. Comparisons of plant productivity. Biol. Review 38: 385-425.

Whittaker, R.H. 1961. Estimation of net primary production of forest and shrub communities. Ecology 42: 177-180.

Whittaker, R.H. 1962. Net production relations of shrubs in the Great Smokey Mountains. Ecology 43: 358-377.

Whittaker, R.H., N. Cohen, and J.S. Olson. 1963. Net production of tree species at Oak Ridge, Tennessee. Ecology 55: 806-810.

Wilde, S.A. 1967. Production of energy materials by forest stands as related to supply of soil water. Silva Fennica 121: 31-44.

Young, H.E. and A.J. Chase. 1965. Fiber weight and pulping characteristics of the logging residues of seven tree species in Maine. Maine Agr. Expt. Sta. Tech. Bull. 17. 44 p.

Young, H.E., L. Strand, and R.A. Altenberger. 1964. Preliminary fresh and dry weight tables for seven tree species in Maine. Maine Agr. Expt. Sta. Tech. Bull. 12. 76 p.

Natural Resources
Library

Thomas R. Crow
Words: 585

ABSTRACT

THE ESTIMATION OF BIOMASS IN A NATURAL STAND OF JACK PINE (PINUS BANKSIANA LAMB.)

The primary objective of this study was to investigate the application of regression techniques as well as the validity of "mean tree" estimates in the determination of biomass in a natural stand of jack pine in north-central Minnesota. A secondary objective was to determine the distribution of biomass among all stand components.

Mean and standard error of mean figures for the target population reflect the relatively small size of the trees and the even-aged character of the stand: mean DBH = 4.77 ± 0.08 inches; mean total height = 38.11 ± 0.42 ft; mean age = 51.32 ± 0.36 years; N = 180. The stand had a basal area of 78.49 ft^2/acre and a site index of 40.6 ft at 50 years.

Forty trees were harvested from the entire size range of the target population and in proportion to the distribution within each crown class. Arboreal samples were subdivided into needles, dead branches, live branches, bole-wood, bole-bark, and roots. Samples of woody, herbaceous, and moss components in the understory vegetation supplemented arboreal samples. To investigate the empirical relationship between biomass and a number of independent variables (DBH, diameter-tree base, diameter-base of contiguous crown, DBH^2, cross-sectional area at tree base, DBH^2 X total tree height (D^2H), total tree height, canopy height, canopy volume), six curve forms were fitted and correlation coefficients calculated:

linear, $Y = A + BX$ (1)

exponential, $Y = Ae^{BX}$ or $\log Y = \log A + BX$ (2)

allometric, $Y = AX^B$ or $\log Y = \log A + B \log X$ (3)

hyperbolic, $Y = X/(A+BX)$ or $1/Y = B + A(1/X)$ (4)

Two forms of multiple regressions were also fitted.

No single curve form or independent variable consistently produced the most reliable fit for all components. The best general form proved to be the allometric curve (3), with DBH as the independent variable. However, for most components, the convenient linear regression could be used with only a slight reduction in reliability. The independent variable DBH proved superior to bole diameter-tree base, bole diameter-base of crown, and canopy volume. Use of canopy height and total tree height as independent variables resulted in relatively low correlations. Because π is a constant, the independent variable DBH^2 should be substituted for cross-sectional area at DBH, regardless of curve form. When using the allometric curve, the same fit is obtained regardless if the independent variable is DBH or DBH^2. Substitution of D^2H for DBH generally did not improve the accuracy of the regression estimate. Little advantage was found in using multiple regressions in place of the simple regression functions.

Stand estimates of oven-dry weight for each tree component were derived from those curve forms and independent variables giving the most reliable estimate. Distribution of plant biomass among all stand components was as follows:

Understory (N = 30)	
woody	771 ± 64 kg/ha (oven-dry weight)
non-woody	322 ± 27 kg/ha
moss-lichen	2482 ± 226 kg/ha
root-rhizome	16074 ± 476 kg/ha
Arboreal	
total tree	71533 kg/ha (based on summation of trees)

Successive improvements were noted with stand estimates based on a tree of mean total height, mean DBH, and mean basal area. Compared to an every-tree summation, total tree biomass was underestimated by 23.4% when based on a tree of mean total height; when based on the tree of mean basal area, total tree biomass was underestimated by only 2.1%, with a maximum deviation of -7.3% for dead branches. Estimates based on the tree of mean bole volume generally over-estimate biomass; total tree biomass was overestimated by 2.8%, with a maximum deviation of +5.0% for cones. Estimates based on individuals at ± one standard deviation from a stand mean are superior to "mean tree" estimates.

"Mean tree" estimates may be valid for certain community structures and study requirements. Deviations of "mean tree" estimates from the every-tree summation for this even-aged, uniform stand are substantially less than those reported for more complex, all-aged stands.

Major Adviser H. Hansen